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FEATURED PAPER

Quantifying the Monetary Value of Alaska National Forests to Commercial Pacific Salmon Fisheries

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Abstract

Forested landscapes support a diversity of ecological processes and organisms having direct value to society. Assessments placing monetary value on forest processes and organisms can help inform management actions affecting these ecosystem services. The temperate rain forest ecoregion along the west coast of North America is home to five species of Pacific salmon *Oncorhynchus* spp. that support subsistence, personal-use, sport, and commercial fisheries. This study aimed to quantify the number and monetary value of commercially caught Pacific salmon originating from Alaska's Tongass and Chugach national forests, two adjacent national forests containing some of the world's largest remaining tracts of intact temperate rain forest. The proportion of commercially harvested wild Pacific salmon originating from streams and lakes within national forest boundaries was estimated by subtracting hatchery salmon and salmon originating outside national forest areas from the total commercial catch. The Tongass and Chugach national forests were major contributors to the overall number and value of commercially caught Pacific salmon in southeastern and southcentral Alaska. From 2007 to 2016 these national forests contributed an average of 48 million Pacific salmon annually to commercial fisheries, with a dockside value averaging US$88 million (inflation adjusted to the base year 2017). These "forest fish" represented 25% of Alaska's commercial Pacific salmon catch for this time period and 16% of the total commercial value. These findings emphasize the importance of Alaska's forest rivers and lakes for sustaining Pacific salmon and can contribute to discussions about alternative land management strategies that might impact Pacific salmon populations and associated commercial salmon fisheries.

Forest lands support multiple ecological processes and diverse assemblages of organisms that have direct and indirect value to society (Godoy and Bawa 1993; de Groot et al. 2002; Penaluna et al. 2017). Clean water, clean air, carbon sequestration, animal viewing, hiking, hunting, and fishing are just a few of the services that forests provide (Brown et al. 2007). These goods and services are frequently considered to be "free" (de Groot et al. 2002). Indeed, services such as clean water and air can be provided at essentially no cost by functioning forests. However, degradation of forests may diminish the capacity of these ecosystems to provide desired services, which can result in negative impacts to society (Stanturf et al. 2014). For example, deforestation of the Amazon has been

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thought to contribute to reduced precipitation (Malhi et al. 2008; Zemp et al. 2017) and associated water shortages in Brazilian cities (Malhi et al. 2008). In our current society, where decisions are frequently driven by economic pressures, managing forest lands to support diverse values can be informed by quantifying the monetary value of these "free" goods and services (Norberg 1999; Knowler et al. 2003).

Pacific salmon *Oncorhynchus* spp. are a good example of organisms that provide direct services to humans in the form of food but that have also been adversely affected by forest management practices (Everest and Meehan 1981; Nehlsen et al. 1991; Lichatowich 2001). The Pacific Northwest of the United States once supported the largest Pacific salmon runs and associated fisheries in the world (National Research Council 1996; Gustafson et al. 2007). However, within a century of European colonization many of these runs were critically imperiled, due in part to logging activities that deteriorated freshwater spawning and rearing habitat (Lichatowich 2001; Lackey 2003). This legacy of forest management—combined with dam construction, overharvest, mining, and urbanization—has resulted in billions spent on hatcheries and other restoration actions aimed at maintaining recreational, commercial, and subsistence fisheries that were once provided by intact ecosystems (Levin et al. 2001; Lackey et al. 2006). Both the United States and Canada now have policies and laws in place to protect wild Pacific salmon, such as requirements for tree buffers along streams and water quality standards (Budd et al. 1987; Richardson et al. 2012). Nevertheless, strong economic pressures still exist that may be at odds with maintaining healthy Pacific salmon habitat, such as intensive timber harvest, mining, and urbanization. Weighing the economic costs and benefits of these activities requires accounting for the value of forest resources—such as Pacific salmon—that might be negatively impacted by development or resource extraction.

Perhaps the largest and most productive "salmon forests" in the world are in Alaska (Baker et al. 1996; Halupka et al. 2000). The Tongass and Chugach national forests in southeastern and southcentral Alaska (Figure 1) represent some of the largest tracts of intact rain forest in the world (Orians and Schoen 2017), and these forests support productive Pacific salmon fisheries. In southeastern Alaska, for instance, commercial fishing and seafood processing is the largest private-sector industry, accounting for 15% of regional employment (McDowell Group 2017). Many of the ocean-caught Pacific salmon that support the fishing industry likely began their lives in forest streams that drain the Tongass and Chugach national forests. Like other forests, these forests—particularly the Tongass—have historically been valued for timber production (Durbin 1999). However, given the importance of Pacific salmon fisheries to Alaska's economy and culture, understanding and quantifying the economic value of salmon that originate from the Tongass and Chugach national forests is also critical (Gillespie et al. 2018).

Our goal was to quantify the monetary value of commercially harvested Pacific salmon from Alaska's national forest lands. Specifically, this study addressed three questions:

1. How many commercially caught Pacific salmon in southeastern and southcentral Alaska originate from lakes, rivers, and streams in the Tongass and Chugach national forests?
2. What is the monetary value of these "forest fish" to commercial fisheries?
3. What proportion of Alaska's commercial Pacific salmon harvest originates from Alaska national forest lands?

This information can be used to weigh management decisions that may adversely impact Pacific salmon, as well as those management actions (e.g., habitat restoration) aimed at improving habitat and restoring functions critical to freshwater salmon productivity. While subsistence, sport, and personal-use fisheries are not included here, estimating the monetary value of commercial fisheries is an important first step towards a more comprehensive socioeconomic valuation of national forests for fisheries production.

METHODS

Study areas.— The Tongass and Chugach national forests are the first and second largest national forests in the United States, with a total area of approximately 97,000 km^2 (Figure 1). The Tongass National Forest covers most of southeastern Alaska and the Alexander Archipelago (69,000 km^2). The Chugach National Forest (28,000 km^2) covers the Copper River delta, Prince William Sound, and part of the Kenai Peninsula. Most of the Tongass and Chugach national forests lie within the temperate rain forest ecoregion and have high levels of precipitation (1,500–5,000 mm on the Tongass and 500–6,000 mm on the Chugach; University of Alaska Fairbanks 2015). This precipitation feeds into streams, rivers, and lakes, supporting five species of commercially important Pacific salmon: Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka*, Pink Salmon *O. gorbuscha*, and Chum Salmon *O. keta*.

The marine environments adjacent to the Tongass and Chugach national forests support lucrative commercial Pacific salmon fisheries. From 2007 to 2016, the total commercial Pacific salmon harvest from the Commercial Salmon Management Areas adjacent to the Tongass National Forest (Southeast Region) and Chugach National Forest (primarily Prince William Sound)

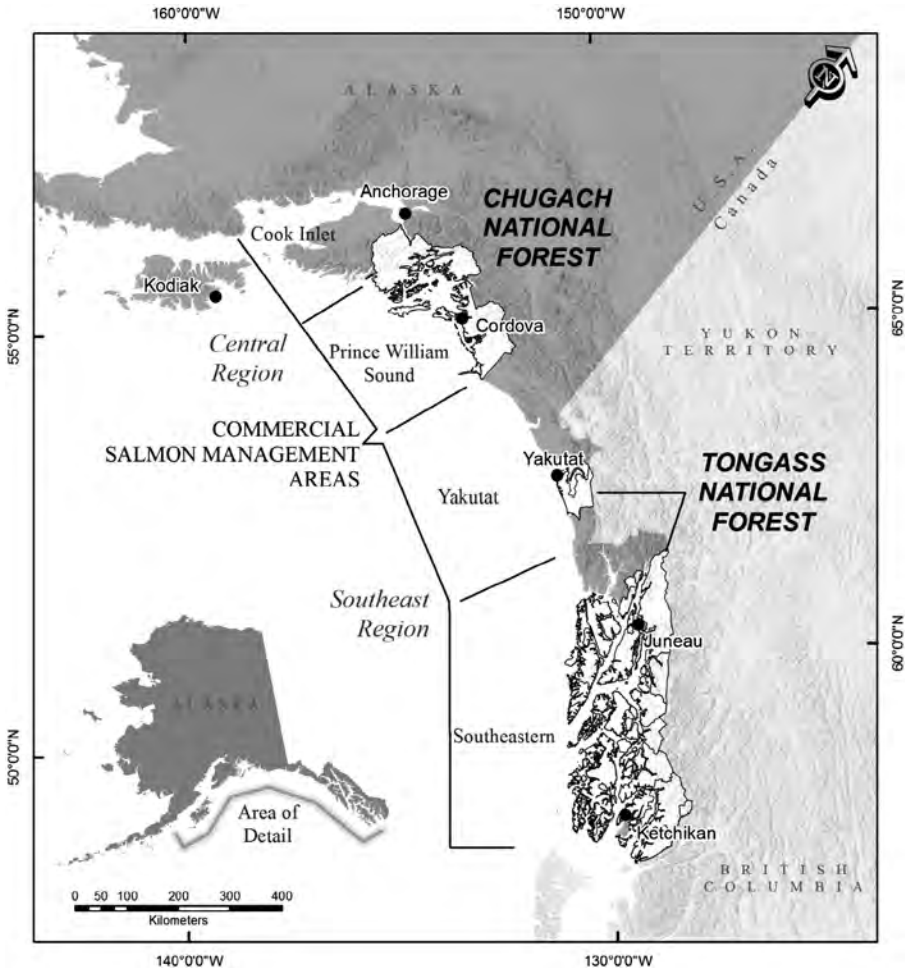

FIGURE 1. Map for the Tongass National Forest and Chugach National Forest (land area indicated in white with black border) and adjacent Alaska Department of Fish and Game Commercial Salmon Management Areas.

generally surpassed 100 million fish per year, with an annual value surpassing US$225 million (Conrad and Gray 2017; Russell et al. 2017). The Pacific salmon caught in these fisheries, however, do not all originate from national forest lands, and depending on the species and region, a large proportion of the fish may originate either from hatcheries or from lands outside Alaska's national forest boundaries. For instance, there are 21 hatchery facilities adjacent to the Tongass and Chugach national forests (Stopha 2017), which produce large numbers of Pacific salmon—primarily Chum Salmon and Pink Salmon—that are harvested in commercial fisheries.

Value assessment approach.— A simple set of calculations was made to estimate the number and monetary value of Pacific salmon originating from the Tongass and Chugach national forests that are harvested in commercial Pacific salmon fisheries. We define "originating from" as those Pacific salmon that emerged from stream gravels within Tongass or Chugach National Forest boundaries. Our approach began by obtaining estimates of the total annual commercial Pacific salmon harvest (*TotalHarvest*) from Commercial Fishing Management Areas adjacent to national forest lands (see Figures 1, 2). These values were then corrected to remove Pacific salmon not originating from either the Tongass or Chugach national forests, as follows:

$$ForestFish_i = TotalHarvest_i \times [1 - (PropHatchery_i + PropOutside_i)] \quad (1)$$

where $ForestFish_i$ represents the number of Pacific salmon of species i originating from national forest lands, $PropHatchery_i$ is the proportion of Alaska hatchery-produced Pacific salmon in the commercial harvest, and $PropOutside_i$ is the proportion of Pacific salmon that originate from streams, rivers, and hatcheries outside Alaska national forest lands. Once the number of Pacific salmon originating from Alaska's national forest lands

($ForestFish_i$) was estimated based on the geographic region, this value was converted to U.S. dollars by multiplying fish numbers by the average weight of each Pacific salmon species and the associated average ex-vessel price (i.e., dockside value) from Alaska Department of Fish and Game (ADFG) data (gross harvest number, weight, and value by species and harvest area; ADFG 2007–2016b). Average price per pound for fish was subsequently adjusted for inflation over time using the consumer price index averaged for U.S. cities (U.S. Department of Labor 2017) using January 2017 as the standard base.

Applying the approach.— We obtained commercial Pacific salmon harvest numbers for 2007–2016 for Commercial Salmon Management Areas adjacent to the Tongass and Chugach national forests from the ADFG statewide electronic fish ticket database (ADFG 2018a). For the Tongass National Forest, this comprised the Southeast Region, specifically the Yakutat Commercial Salmon Management Area and Southeastern Commercial Salmon Management Area (Figure 1). For the Chugach National Forest, this comprised the Central Region, specifically the Prince William Sound Commercial Salmon Management Area and a small portion (<10%) of the Cook Inlet Commercial Salmon Management Area, including the upper portion of Turnagain Arm west of Anchorage and a portion of the Kenai River draining into Cook Inlet (see Figure 1; Supplement A available in the online version of the article). In general, national forest boundaries and Commercial Salmon Management Areas closely overlapped (Figure 1). We then adjusted commercial Pacific salmon harvest numbers ($TotalCatch_i$) for these management areas using equation (1).

The proportion of the commercial Pacific salmon harvest that was of hatchery origin ($PropHatchery_i$) was determined from queries of ADFG databases with interpretation by ADFG fish biologists for 2006–2017 and other relevant references (Mark Stopha, Assistant Coordinator, Private Nonprofit Hatchery Program; Table 1; Supplement B available in the online version of the article). Most Alaska hatcheries thermally mark, chemically mark, or coded-wire-tag juvenile fish (ADFG 2007–2016a; see also Volk et al. 1999) as a means for ADFG to apportion hatchery harvest by origin. Estimates of commercially harvested, hatchery-origin fish were used in the calculation of nonforest fish for Chinook, Coho, Sockeye, Pink, and Chum salmons. Hatchery proportions included Pacific salmon harvested for hatchery brood stock and cost recovery (i.e., Pacific salmon harvested to pay for hatchery operations), as well as commercial common property fishery harvests.

The proportion of Pacific salmon that originated outside of national forest lands ($PropOutside_i$; Table 1) was estimated via two different approaches. In the Central Region (Prince William Sound and a portion of the Cook Inlet subregions), the proportion of Pacific salmon that did not originate from the Chugach National Forest was evaluated using the Alaska Anadromous Waters Catalog (AWC; Johnson and Blossom 2017; ADFG 2018b). We used the AWC to calculate the proportion of documented spawning habitat located outside Chugach National Forest boundaries. It was assumed that the proportion of spawning habitat outside of Chugach National Forest lands represented the fraction of Pacific salmon harvested from nearby fisheries that did not originate from neighboring national forest lands. It is important to note this approach assumes that all documented Pacific salmon streams produce the same number of salmon per unit distance of cataloged spawning habitat; we assumed this to be a reasonable assumption when averaging across the entire region. For the Southeast Region (Southeastern and Yakutat subregions), calculations using the AWC were not

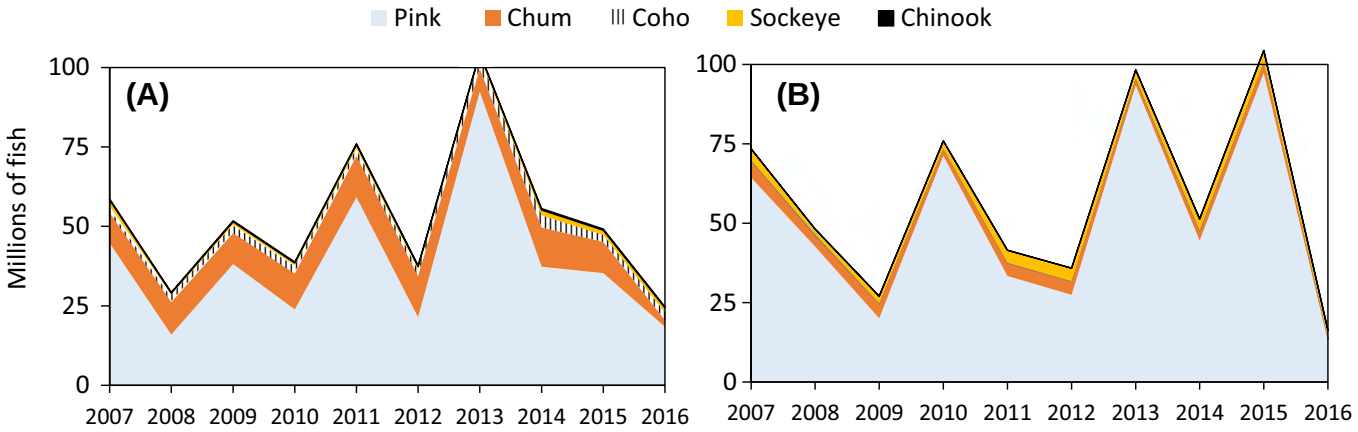

FIGURE 2. Total commercial harvest of Pacific salmon off shore from **(A)** the Tongass National Forest (Southeast Region Commercial Management Area, including Yakutat subregion) and **(B)** the Chugach National Forest (Prince William Sound subregion plus the Copper River and a portion of upper Cook Inlet).

TABLE 1. Estimates of the average percent and range of Pacific salmon caught in commercial fisheries from 2007 to 2016 that did not originate from the Tongass National Forest (within Southeast Region) or Chugach National Forest (within Central Region). Estimates include Pacific salmon from hatcheries and Pacific salmon originating from lands outside Tongass and Chugach National Forest boundaries. Ranges represent the minimum and maximum estimates for the 10-year period. Data is summarized from Alaska Department of Fish and Game reports and personal communication (see Methods for details).

Species and Commercial Salmon Management Area	Average percent fish from Alaska hatcheries (range)	Average percent fish from Washington, Oregon, Canada, or outside national forest lands (range)	References and personal contacts for sources of Alaska Department of Fish and Game data
Chinook Salmon			
Southeast Region	29 (16–42)	67 (55–80)	Hatchery data (Mark Stopha); Southeast Region forest fish (Peterson et al. 2017); Yakutat area (Nicole Zeiser); transboundary river information (Pacific Salmon Commission 2017); Glacier Bay (Dave Harris); Chilkat River (Richard Chapell)
Central Region	0 (no range)	93 (86–97)	Prince William Sound Region and Copper River contribution (Stormy Haught); Cook Inlet contribution (Mark Willette)
Sockeye Salmon			
Southeast Region	17 (10–28)	60 (47–66)	Hatchery data (Mark Stopha); Yakutat area (Nicole Zeiser); transboundary river information (Pacific Salmon Commission 2017, Steve Heinl, Troy Thynes, Julie Bednarski); Glacier Bay (Dave Harris); Taku, Chilkoot, Chilkat (Steve Heinl)
Central Region	44 (35–65)	25 (12–33)	Prince William Sound and Copper River contribution (Stormy Haught); Cook Inlet contribution (Mark Willette)
Coho Salmon			
Southeast Region	31 (24–39)	2 (1–5)	Hatchery data (Mark Stopha); Yakutat area (Nicole Zeiser); transboundary river information (Pacific Salmon Commission 2017); Glacier Bay (Dave Harris)
Central Region	23 (3–39)	16 (13–18)	Prince William Sound and Copper River contribution (Stormy Haught); Cook Inlet contribution (Mark Willette)
Pink Salmon			
Southeast Region	3 (1–6)	2 (0–6)	Hatchery data (Mark Stopha); Yakutat area (Nicole Zeiser); transboundary river information (Pacific Salmon Commission 2017); Glacier Bay (Dave Harris); Taku, Chilkoot, Chilkat (Steve Heinl)
Central Region	87 (74–97)	1 (0–3)	Prince William Sound and Copper River contribution (Stormy Haught); Cook Inlet contribution (Mark Willette)
Chum Salmon			
Southeast Region	84 (78–91)	1 (0–1)	Hatchery data (Mark Stopha); Yakutat area (Nicole Zeiser); transboundary river information (Pacific Salmon Commission 2017); Glacier Bay (Dave Harris); Taku, Chilkoot, Chilkat (Steve Heinl)
Central Region	94 (83–97)	1 (0–1)	Prince William Sound and Copper River contribution (Stormy Haught); Cook Inlet contribution (Mark Willette)

feasible for two reasons. First, much of the spawning habitat lies in large transboundary rivers in Canada and, thus, is not included in the AWC (Alsek, Stikine, and Taku rivers). Second, significant proportions (>50%) of Chinook Salmon harvested in the Southeast Region originate from Oregon, Washington, or southern British Columbia (Peterson et al. 2017). Rather than using the AWC, in the Southeast Region $PropOutside_i$ was based on expert opinion from local ADFG fisheries biologists. Making these estimates required combining harvest information and expert opinion from numerous fishing districts and subdistricts across southeastern Alaska. These $PropOutside_i$ estimates accounted for Pacific salmon originating from a variety of non-national-forest lands, including the following: (1) Glacier Bay and Wrangell–St. Elias national parks, (2) transboundary rivers that originate in Canada (Alsek, Stikine, and Taku rivers), and (3) Pacific salmon from outside the region (Oregon, Washington, and southern British Columbia) that may have returned to natal streams had they not been intercepted by Alaskan fisheries. All $PropOutside_i$ and $PropHatchery_i$ values for 2007–2016 are reported in Supplement B, and the assumptions underlying these proportions are detailed in Supplement A.

To understand how uncertainty in $PropOutside_i$ and $PropHatchery_i$ might influence our estimates, we conducted an uncertainty analysis (Manly 2007). To do this we assumed that the true value for each proportion was plus or minus 10% of the estimated value. For example, in 2016 we estimated that 64% of Sockeye Salmon caught in southeastern Alaska were progeny of fish that spawned outside of national forest lands, with an associated uncertainty range of 54–74%. When proportions were less than 10% or greater than 90%, the uncertainty range was capped at 0% and 100%, respectively. These ranges represent the general magnitude of uncertainty we expected in our proportions (which in some cases were coarse) and, thus, provided a reasonable assessment of how this uncertainty affects our estimates. We used these ranges to calculate 1,000 separate estimates of the total number and monetary value of Pacific salmon from national forest lands, whereby we randomly selected values of $PropOutside_i$ and $PropHatchery_i$ within the specified range assuming a uniform distribution. We used these 1,000 separate estimates to create uncertainty ranges for the total number and monetary value of Pacific salmon from the Tongass and Chugach national forests. Reported uncertainty values represent the 2.5 and 97.5 percentile values of the 1,000 estimates (i.e., 95% of the 1,000 estimates of fish number and value lie within between these values).

RESULTS

Total Pacific salmon harvests from Commercial Salmon Management Areas adjacent to the national forest lands totaled nearly 110 million fish annually, from 2007 to 2016 (Figure 2). During the 10-year study period, >70% of the harvest was Pink Salmon in both regions. Of the remaining Pacific salmon, on average, <20% was Chum Salmon (19% from Southeast Region, 5% from Prince William Sound subregion), <5% was Coho Salmon, <5% was Sockeye Salmon, and <1% was Chinook Salmon.

For the 10-year study period, the Tongass and Chugach national forests contributed, on average, approximately 44% of the Pacific salmon harvested from these Commercial Salmon Management Areas. From 2007 to 2016, an average of 48 million Pacific salmon originating (i.e., emerged as fry) from the Tongass and Chugach national forests were caught annually in Alaskan commercial Pacific salmon fisheries (Figure 3A; see Supplement B). In our uncertainty analysis, average forest contributions to commercial fisheries ranged between 35 to 53 million Pacific salmon annually for the 10-year study period, or approximately ±25% of our reported value (assuming 10% uncertainty in value of the proportions used to calculate our estimate; see Supplement C available in the online version

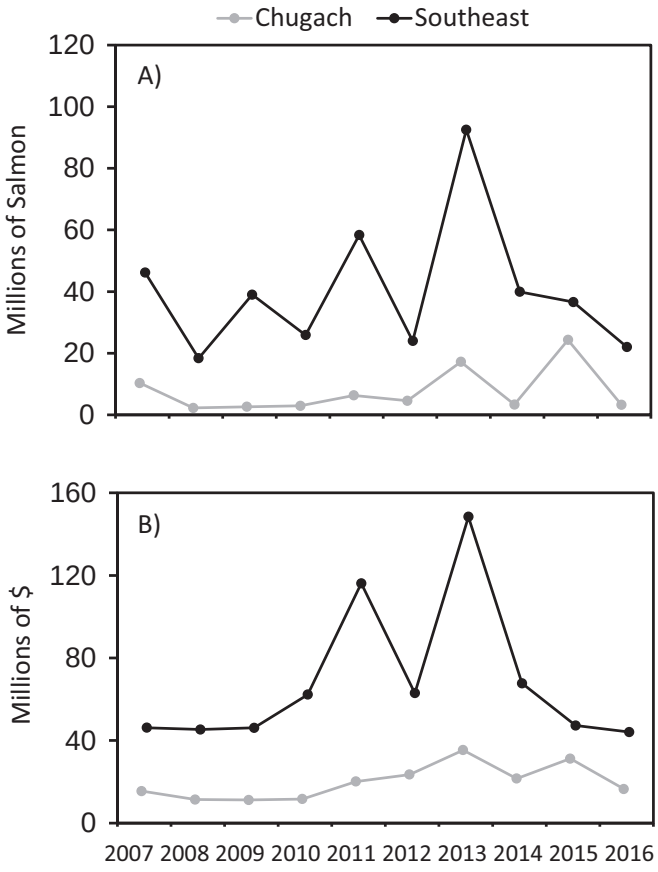

FIGURE 3. Estimates of the **(A)** total number and **(B)** value of Pacific salmon harvested in Alaska's commercial fisheries from 2007 to 2016 that originated from either the Chugach National Forest or the Tongass National Forest (Southeast Region).

of the article for annual values of uncertainty for 2007–2016). On average, these Pacific salmon had a dockside value of $88 million (Figure 3B), with an average annual uncertainty range of $63 to $98 million for the 10-year study period (Supplement C). Compared to the statewide commercial Pacific salmon harvest for 2007 to 2016, these "forest fish" represented, on average, approximately 25% of Alaska's total commercial Pacific salmon harvest number and 16% of the total value.

There were significant differences in the commercial harvest and value of Pacific salmon originating from the Tongass and Chugach national forests (Figure 3). Although the total commercial harvest in marine environments adjacent to the Tongass and Chugach national forests was similar (Figure 2), a much greater proportion of regional commercial Pacific salmon harvests originated from the Tongass National Forest than from the Chugach National Forest (75% average versus 13% average, respectively; Figure 4). This discrepancy was largely due to differences in the percentage of hatchery fish in the commercial harvests (Figure 4). On average for the 10-year study period, hatchery fish represented 21% of the commercial harvest in the Southeast Region (adjacent to the Tongass National Forest) but 84% of the commercial Pacific salmon harvest in the Prince William Sound subregion adjacent to the Chugach National Forest.

Although there was substantial year-to-year variation in the amount of Pacific salmon originating from the Tongass and Chugach national forests (Figure 3A), Pink Salmon were—by far—the most numerically dominant "forest fish" comprising the commercial Pacific salmon harvest (Figure 5). On average, Pink Salmon represented approximately 91% (37 million) and 83% (6.4 million) of the total commercial harvests from the Tongass and Chugach national forests, respectively. For the Tongass

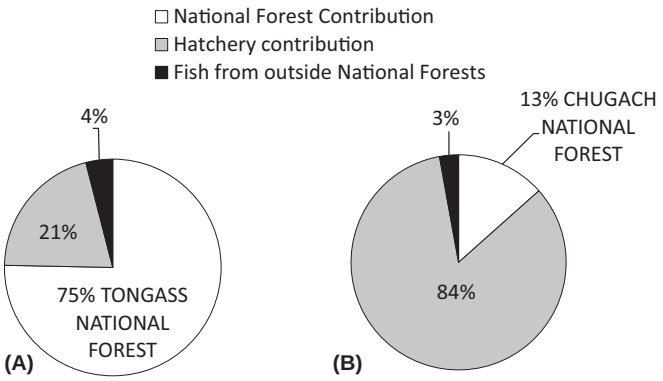

FIGURE 4. Pie charts showing the origin of Pacific salmon caught off shore from **(A)** the Tongass National Forest (Southeast Region) and **(B)** the Chugach National Forest (Prince William Sound subregion).

National Forest, Chum Salmon averaged 3% (1.6 million), Coho Salmon averaged 4% (11.8 million), Sockeye Salmon averaged <1% (276,000), and Chinook Salmon represented <0.1% (13,000) of commercial harvests. On the Chugach National Forest, Sockeye Salmon represented nearly 15% (922,000) of the commercial harvest, Coho Salmon averaged 4% (245,000), Chum Salmon averaged 2% (157,000), and Chinook Salmon averaged 0.01% (1,000).

From 2007 to 2016, the average Pacific salmon commercial value (in U.S. dollars) ranged from a low of $0.31 per pound for Tongass National Forest Pink Salmon to a high of $5.50 per pound for Chugach National Forest Chinook Salmon (Figure 6). Average price per pound of both Chum Salmon and Coho Salmon was higher for fish from the Tongass National Forest than for those from the Chugach National Forest ($0.65 versus $0.60 and $1.23 versus $1.07, respectively). Average price per pound of Pink, Sockeye, and Chinook salmons was higher for fish

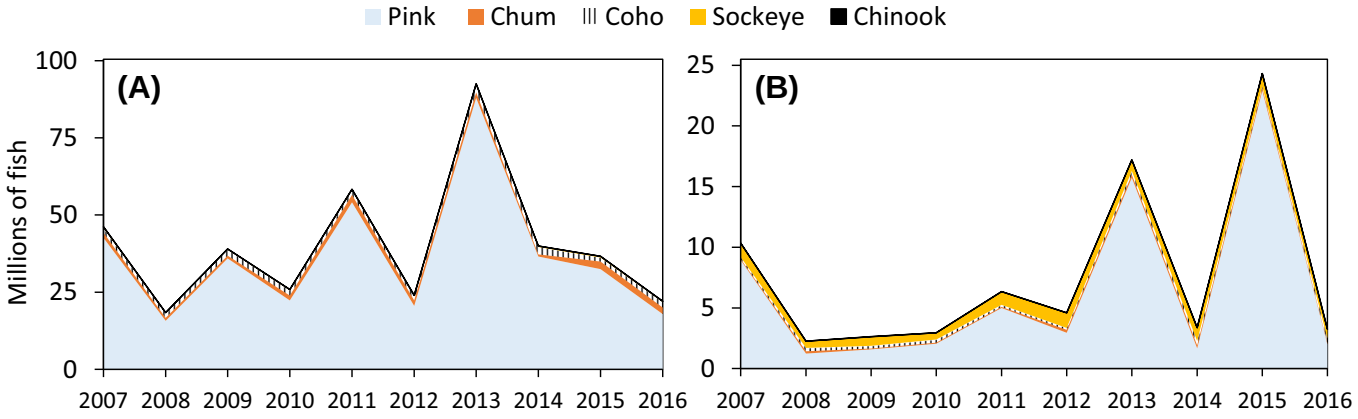

FIGURE 5. Estimated number of each Pacific salmon species originating from the **(A)** Tongass National Forest and **(B)** Chugach National Forest that are commercially harvested.

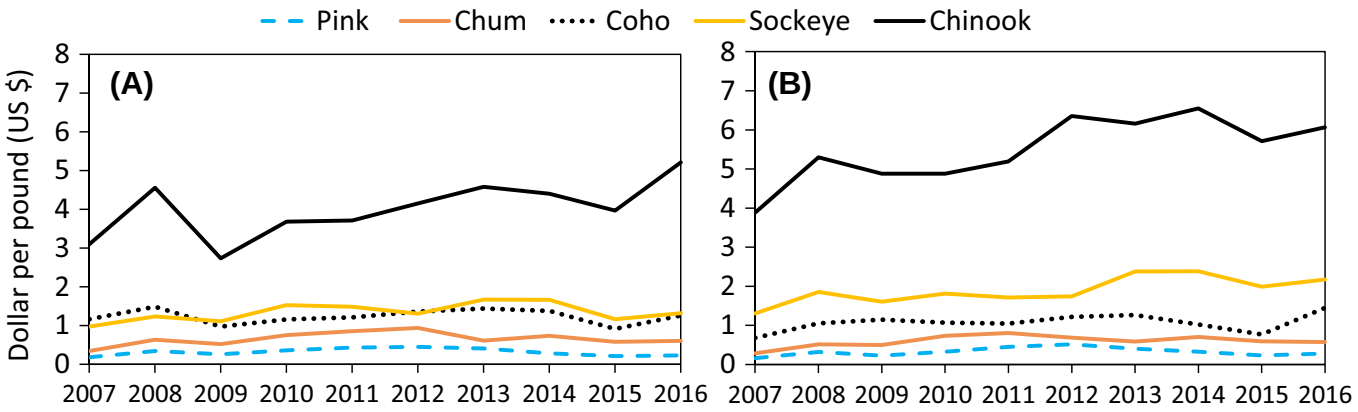

FIGURE 6. Average dockside price per pound paid for different Pacific salmon species harvested off shore from **(A)** the Tongass National Forest (Southeast Region) and **(B)** the Chugach National Forest (Prince William Sound subregion). Note that the price per pound for fish was adjusted for inflation.

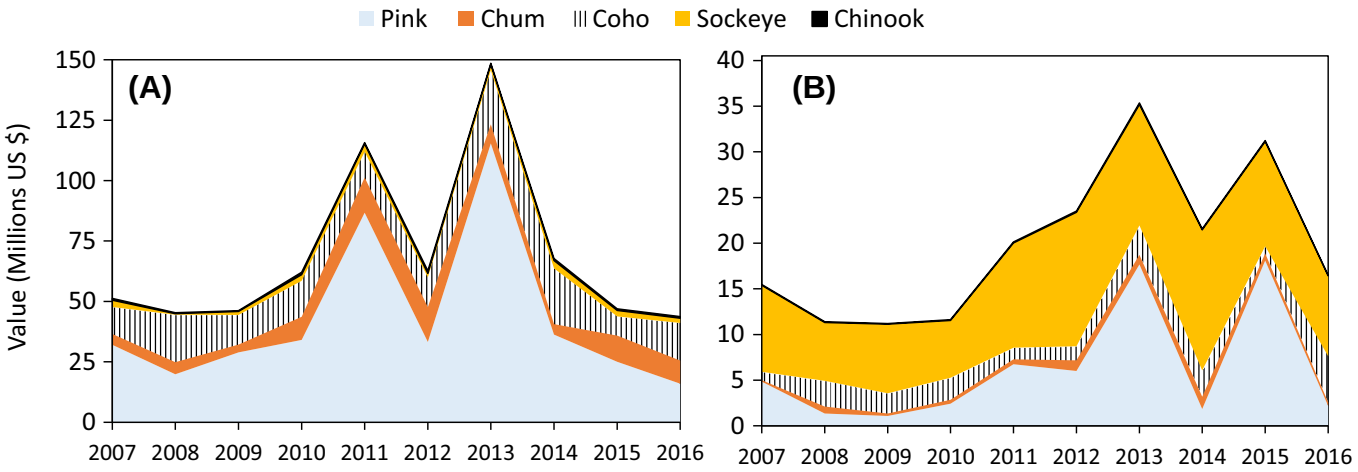

FIGURE 7. Estimated dockside value of each Pacific salmon species from the **(A)** Tongass National Forest and **(B)** Chugach National Forest that are commercially harvested.

from the Chugach National Forest than for those from the Tongass National Forest ($0.33 versus $0.31, $1.90 versus $1.34, $5.50 versus $4.00, respectively).

Pink Salmon originating from the Tongass National Forest, averaging $42 million annually for the study period, had the greatest overall value. Sockeye Salmon, averaging $10.5 million annually, had the highest total value on the Chugach National Forest (Figure 7). On the Tongass National Forest, the value of Chum, Coho, Sockeye, and Chinook salmons averaged $8.8 million, $14.8 million, $2.2 million, and $676,000, respectively, during the 10-year study period. On the Chugach National Forest, the value of Pink, Chum, Coho, and Chinook salmons averaged $6.2 million, $694,000, $2.3 million, and $107,000, respectively.

DISCUSSION

Using 2007 to 2016 existing fisheries data, we estimated the monetary value of Alaska's national forest lands to commercial Pacific salmon fisheries. We found that the Tongass and Chugach national forests—the largest national forests in the United States—were major contributors to the overall number and value of commercially caught Pacific salmon in southeastern and southcentral Alaska. In turn, these commercial fisheries are significant contributors to community well-being and the regional economy (e.g., Smith and Clay 2010; TCW Economics 2010; ASMI 2011; Gillespie et al. 2018). Alaska typically accounts for 12–15% of the global supply of Pacific salmon (ASMI 2011), and the Tongass and Chugach national forests, with a land area less than 100,000 km^2,

contributed an estimated 25% of the state's commercial Pacific salmon harvest. These findings further emphasize the importance of forest rivers and lakes for sustaining healthy fisheries (Goulding 1980; Naiman et al. 2000; Tanentzap et al. 2014).

Our estimates of the value of Pacific salmon from the Tongass and Chugach national forests can contribute to discussions about alternative land management strategies that might adversely impact salmon populations and associated commercial fisheries (e.g., road building, mining, and logging), as well as those management strategies aimed at improving forest conditions for Pacific salmon (e.g., habitat restoration). Moreover, our estimates provide the basis for a more inclusive evaluation of the socioeconomic value of Pacific salmon from forests that include sport, personal-use, and subsistence fisheries, as well as the indirect value of these fish to local communities.

Our analysis showed that Pink Salmon and Sockeye Salmon were the highest-commercial-value Pacific salmon species originating from forest lands on the Tongass National Forest and Chugach National Forest, respectively. The high value of Pink Salmon from the Tongass National Forest resulted from their numerical abundance. Despite their small size and lower price per pound, Pink Salmon were over an order of magnitude more abundant in the commercial catch than any other Pacific salmon species. Relative to Chinook Salmon, for instance, Pink Salmon were one-quarter the size, one-third the value, but 100 times more numerous. Pink Salmon also dominated commercial Pacific salmon harvests from the Chugach National Forest during the 10-year study period; however, Sockeye Salmon had a higher overall value due to the greater weight and higher price per pound of Sockeye Salmon relative to Pink Salmon (10-year average of $0.33 versus $1.90 per pound). Nevertheless, Pink Salmon were still the highest-value Pacific salmon derived from both national forests combined because of the total weight of the catch. That said, it is important to acknowledge that Chinook, Sockeye, and Coho salmons are more important for sport, subsistence, and personal-use fisheries (e.g., Jennings et al. 2007; Conitz 2008) because they are preferred and targeted by these user groups.

This study helped to clarify the magnitude of hatchery Pacific salmon harvests adjacent to national forest lands, particularly in the commercial fishing region adjacent to the Chugach National Forest, where hatchery fish comprised, on average, over 84% of the commercial harvest (versus 21% adjacent to the Tongass National Forest) for the study period. Hatcheries were established in the 1970s to rehabilitate depleted Pacific salmon fisheries. That said, concerns about hatchery effects on wild Pacific salmon populations are rising, warranting further review of multiple ecological and genetic interactions associated with hatcheries (Evenson et al. 2018). The concerns include the impacts of hatchery strays on wild stock population structure and productivity (Gorman et al. 2018), competition between hatchery- and wild-origin juvenile Pacific salmon and resulting density-dependent effects (Holt et al. 2008; Ruggerone et al. 2012; Lewis et al. 2015; Sergeant et al. 2017), and complications for wild-stock fisheries management (Evenson et al. 2018). Despite concerns about the potential effects of hatchery fish on wild fish, from a commercial fishery perspective, hatchery and wild fish are generally indistinguishable and thus have the same monetary value.

Despite their value, Pacific salmon are susceptible to the economic pressures of resource extraction (e.g., logging, mining; Beschta et al. 1987; Baker and McLelland 2003; Crone 2005; Scannell 2012) and development (e.g., dam construction, urbanization; Taylor 2002). These activities have contributed to the loss of populations of Atlantic Salmon *Salmo salar* across most of their historic range, as well as dramatic declines in Pacific salmon—particularly in the contiguous USA (California, Oregon, and Washington) (Nehlsen et al. 1991; Lichatowich 2001; Montgomery 2003). Although Alaskan Pacific salmon populations remain relatively healthy, these populations are susceptible to the same set of factors that have led to declines in other regions (Schoen et al. 2017). Moreover, these populations will have to contend with rapid environmental changes associated with climate change, which may negatively impact the capacity for forest streams to sustain Pacific salmon via a variety of mechanisms (Bryant 2009; Shanley and Albert 2014; Sergeant et al. 2017; Sloat et al. 2017). Our findings illustrate that reductions in the capacity of forest streams to produce Pacific salmon could have consequences for commercial fisheries, as well as the regional economy.

We acknowledge that assessing the number and value of Pacific salmon from national forests to commercial salmon fisheries required making numerous assumptions about the proportion of hatchery-origin fish, as well as fish that emerged from streams outside national forest boundaries. Our analysis would no doubt benefit from a more robust examination of these assumptions. In particular, better evaluation of the proportion of Pacific salmon harvests that did not originate from national forest lands ($PropOutside_i$) would improve our estimates. Nevertheless, our uncertainty analysis suggested that even relatively substantial changes to these proportions (±10%) do not dramatically modify our overall findings. Moreover, because our analysis was restricted to Pacific salmon that originated—i.e., emerged from the gravel as fry—on national forest lands, our estimates of Pacific salmon number and value from national forests to the commercial fishery could be considered conservative. Our estimates do not account for the numerous pathways by which forests support Pacific salmon. For instance, Pacific salmon fry that emerge upstream of national forest lands (e.g., in

transboundary rivers and large watersheds like the Copper River) will migrate downstream and may utilize rivers, lakes, and estuaries within national forest boundaries for rearing (e.g., Murphy et al. 1997). Streams and rivers in southeastern and southcentral Alaska also contribute massive fluxes of nutrients, organic matter, and organisms to the marine environment that may support ocean Pacific salmon productivity via numerous energetic pathways (Tanentzap et al. 2014; O'Neel et al. 2015; Whitney et al. 2018). Finally, and perhaps most importantly, our study does not account for subsistence, personal-use, and sport fisheries, which are extremely valuable to local communities, the regional economy, and the Alaskan way of life (TWC Economics 2010).

Management Implications and Conclusions

These analyses can be updated into the future to track changes in the number and value of forest salmon caught in the commercial fishery. In turn, this information can be used to communicate the value of Alaska's national forests for fish production and can contribute to discussions about management decisions that might influence the capacity of these forests to sustain Pacific salmon in the future. Furthermore, this study provides a starting point for more extensive analyses of salmon production from Alaska's national forest lands. Next steps could include further assessment of the value of sport, personal-use, and subsistence fisheries as well as the nonmonetary value of Pacific salmon to communities and culture. Additional research is needed to understand the mechanistic pathways by which forests support Pacific salmon production. In particular, food web studies are needed that illuminate the flows of energy and nutrients from forests to fish (e.g., Wipfli and Baxter 2010; Tanentzap et al. 2014; Rine et al. 2016). For example, in an Amazonian river, Correa and Winemiller (2014) found that both forest plant material and insects from the forest canopy were major contributors to fish diets. By understanding how forest streams support fish production, a value can be placed on the intermediate ecosystem goods and services (Boyd and Banzhaf 2007), such as aquatic macroinvertebrate diversity (Daniels et al. 2019), that are important for sustaining forest fishes.

We illustrate that Pacific salmon that originate from Alaska's national forests represent a substantial proportion of the number and value of Pacific salmon harvested in regional commercial fisheries. The Alaska salmon industry harvests enough Pacific salmon to feed every human on the globe at least one salmon meal per year (McDowell Group 2017), and our analysis suggests that for the 2007–2016 study period the Tongass and Chugach national forests contributed to at least 25% of this harvest. Although Pacific salmon populations are currently relatively healthy in Alaska, the forests that contribute to Pacific salmon production encounter the same threats that have led to the decline of Pacific salmon populations in other regions (e.g., habitat destruction and damming, mining, hatchery interactions, overharvest; Schoen et al. 2017). Moreover, ongoing climate change has the potential to significantly affect freshwater and saltwater habitats and associated Pacific salmon populations (Mueter et al. 2002; Bryant 2009; Brander 2010; Johnson et al. 2019). Maintaining the capacity for these and other forests to support healthy Pacific salmon will require adaptive learning and preserving the processes that create habitat complexity, including natural disturbances such as floods and landslides (Reeves et al. 1995; Johnson et al. 2000; Benda et al. 2003, 2004; Miller and Burnett 2008), factors promoting a diversity of Pacific salmon species and life histories that may be necessary to maintain productive and adaptive Pacific salmon populations in a changing world (Schindler et al. 2003; Moore et al. 2010; Schoen et al. 2017).

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Effects of Roads on Hydrology, Geomorphology, and Disturbance Patches in Stream Networks

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Abstract: *We outline a view of how road networks interact with stream networks at the landscape scale and, based on examples from recent and current research, illustrate how these interactions might affect biological and ecological processes in stream and riparian systems. At the landscape scale, certain definable geometric interactions involving peak flows (floods) and debris flows (rapid movements of soil, sediment, and large wood down steep stream channels) are influenced by the arrangement of the road network relative to the stream network. Although disturbance patches are created by peak-flow and debris-flow disturbances in mountain landscapes without roads, roads can alter the landscape distributions of the starting and stopping points of debris flows, and they can alter the balance between the intensity of flood peaks and the stream network's resistance to change. We examined this conceptual model of interactions between road networks and stream networks based on observations from a number of studies in the H. J. Andrews Experimental Forest, Oregon (U.S.A.). Road networks appear to affect floods and debris flows and thus modify disturbance patch dynamics in stream and riparian networks in mountain landscapes. We speculate that these changes may influence the rates and patterns of survival and recovery of disturbed patches in stream networks, affecting ecosystem resilience, and we outline an approach for detecting such effects based on a patch dynamics perspective. A field sampling scheme for detecting the magnitude of various road effects on stream and riparian ecology could involve (1) landscape stratification of inherent stream network susceptibility to floods or debris flows, (2) overlay of road and stream networks and creation of areas with various densities of road-stream crossings, emphasizing midslope road-stream crossings, and (3) designations of expected high- and low-impact stream segments based on numbers of upstream road-stream crossings where sampling of selected biological variables would be conducted.*

Efectos de Carreteras en la Hidrología, Geomorfología y Parches de Perturbación en Redes de Arroyos

Resumen: *Desglozamos una perspectiva sobre la interacción entre redes carreteras y redes de arroyos a escala de paisaje e ilustramos como estas interacciones pueden afectar procesos biológicos y ecológicos en sistemas de arroyos y riparios en base a ejemplos que parten de investigaciones recientes y en proceso. A escala de paisaje, ciertas interacciones geométricas definibles y que involucran flujos-pico (inundaciones) y flujos de detritus (movimientos rápidos de suelo, sedimentos y piezas grandes de madera en canales con pendiente pronunciada) son influenciadas por los arreglos de la red de carreteras en relación con la red de arroyos. A pesar de que los parches de perturbación son creados por perturbaciones en los flujos-pico y en los flujos de detritus en paisajes montañosos sin carreteras, las carreteras pueden alterar las distribuciones de puntos de inicio y final de flujos de detritus en el paisaje y pueden alterar el balance entre la intensidad de los picos de inundación y la resistencia del arroyo al cambio. Examinamos este modelo conceptual de interacciones entre la red de arroyos y la red de carreteras en base a observaciones de una cantidad de estudios del Bosque Experimental Andrews, en Oregon. Las redes de carreteras aparentemente afectan las inundaciones y los flujos de detritus, esto modifica la dinámica de los parches de perturbación en redes de arroyos y zonas riparias de paisajes montañosos. Especulamos que estos cambios pueden influenciar las tasaa y patrones de*

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supervivencia y recuperación de parches perturbados en redes de arroyos, afectando la resistencia del ecosistema y detallamos una aproximación para detectar estos efectos en base a una perspectiva de dinámica de parches. Un esquema de muestre de campo para detectar la magnitud de varios efectos de las carreteras en la ecología de arroyos y zonas riparias podría involucrar (1) la estratificación de la susceptibilidad inherente de la red de arroyos a inundaciones o flujo de detritus en el paisaje, (2) la sobreposición de redes de arroyos y carreteras y la creación de cruces a mitad de la pendientes, y (3) la designación de segmentos esperados de bajo y alto impacto donde se realicen muestreos de variables biológicas selectas en base a números de cruces entre arroyos y carreteras que se encuentren arroyo arriba.

Introduction

Road networks have a great variety of effects on watersheds. Most existing studies of road effects on ecosystems are fine in scale and focus on terrestrial ecosystems (Forman & Alexander 1998). Landscape-scale studies of roads have emphasized "zones of influence" of roads extending laterally into terrestrial ecosystems (e.g., Forman & Deblinger, 2000). We offer a complementary approach that considers the effects of road networks on stream and riparian networks. This perspective is based on experience in steep mountain watersheds with high precipitation, forest cover, and road networks constructed for forestry land use, but the principles may apply to other ecosystems.

Early work in geomorphology (Horton 1945; Leopold et al. 1964) laid the groundwork for studies of network structure and associated hydrologic and geomorphic processes, and recent studies (e.g., Montgomery & Dietrich 1988, 1992) explain aspects of complex natural stream channel networks from elementary physical principles. Geomorphology studies in mountain stream networks, especially along the Pacific coast of the United States, emphasize a spatially and temporally explicit view of geomorphic processes, exploiting the availability of digital elevation data and capabilities of geographic information systems to examine landforms, streams, and geomorphic processes.

Stream networks collect episodic inputs of sediment and wood, provided by landslides and other processes, and transport this material episodically through a channel network (Jacobson 1995; Benda & Dunne 1997*a*, 1997*b*). Over time, especially during floods, the physical features of the stream—channels, bars, and floodplains—are created and modified by interactions among sediment, water, and wood (Lyons & Beschta 1983; Grant 1986; Wondzell & Swanson 1999). Thus the patch dynamics of stream networks and riparian forests reflect the history of hydrologic and geomorphic processes (Swanson et al. 1997; Benda et al. 1998).

Two key processes—floods (peak flows) and debris flows—have major influences on riparian vegetation patch dynamics in mountain landscapes, but they produce somewhat different spatial patterns of disturbance in stream and riparian networks. A peak streamflow event is triggered by a pulse of water input from precipitation and/or snowmelt routed through hillslopes and channels to produce a flood wave. Because flood waves are temporally continuous phenomena, peak flow events must be defined arbitrarily from the hydrograph, but the magnitude of each peak (its maximum height) can be determined precisely by field observations or stream gaging. Also, peak flows propagate downstream great distances and have longitudinally extensive zones of impact. Typically, a flood wave creates visibly disturbed patches in the stream network only where its damaging force exceeds local resistance to change; this balance between flood wave force and local resistance is influenced by several factors. Narrow bedrock zones or areas where the stream has been "hardened" (e.g., by roadfill) are less susceptible to disturbance, whereas stream segments below bends or in widened reaches have deposits of relatively fine sediment and colonizing vegetation that are less resistant to modification by the stream's energy (Grant & Swanson 1995).

Debris flows are rapid movements of soil, sediment, and organic matter (large wood) down steep stream channels. Debris flows most commonly originate from debris slides, which are rapid movements (velocities of approximately 10 m per second) of soil, sediment, and associated vegetation down hillslopes. In contrast to peak flows, debris flows produce discrete tracks of channel and riparian disturbance whose number and density per unit area can be precisely estimated, but the volumes of sediment moved may be difficult to measure because (among other difficulties) they may be removed by streamflow. Debris flow tracks can be mapped because they have distinct starting points, a relatively clearly defined zone of primary impact, and an identifiable stopping point. Individual tracks may reach tens of meters in width and several kilometers in length (Swanson et al. 1998; Snyder 2000; Nakamura et al. 2000). The location and proximal cause of individual debris flows also can be interpreted in the field, so they lend themselves to analyses of numbers, locations, and the types of patches created in a stream network.

Flood peaks and debris flows are hydrologic and geomorphic processes with landscape-scale expressions in the stream network that create aquatic and riparian patch dynamics critical to stream ecosystems (Pringle et al. 1988). The creation, destruction, and modification of

stream geomorphic features such as channels, bars, and floodplains are tightly coupled with biotic features including riparian vegetation and lotic and benthic communities (Pringle et al. 1988; Swanson et al. 1988; Gregory et al. 1991). Stream organisms such as salmonids may be tied to the historical disturbance pattern over evolutionary time (Reeves et al. 1995), over multiple generations of spawning at a given site (Geist & Dauble 1998), or even at the scale of an individual spawning salmon (Montgomery et al. 1996). Infrequent, intense flooding is believed to produce larger, more severely disturbed stream and riparian patches than frequent, less intense flooding (Gregory et al. 1991; Michener & Haeuber 1998; Swanson et al. 1998). A reduction in severe, infrequent floods (e.g., by reservoir operations) reduces off-stream habitat for endangered fishes, whereas experimental floods increase it (Schmidt et al. 1998; Pitlick & Van Steeter 1998; Van Steeter & Pitlick 1998). In other words, native stream organisms appear to be linked integrally to the natural disturbance regime (sensu Reeves et al. 1995; Swanson et al. 1997) and the natural streamflow regime (sensu Poff et al. 1997).

Road networks constructed for forest harvest in the Pacific Northwest appear to have increased the magnitude and frequency of peak flows, debris slides, and debris flows relative to those in areas that are fully forested and fire-disturbed. Road construction is associated with increased frequency of landslides and other forms of erosion in steep forest landscapes (Swanson & Dyrness 1975; Nolan et al. 1995). A variety of mass movement and fluvial processes have been noted along road networks after intense flooding in this landscape (Wemple 1998). Increases in peak discharges have been significantly associated with forest harvest and road construction in both small experimental basins (<1 km^2) and in large basins (60–600 km^2) over the past 4–6 decades (Jones & Grant 1996; Thomas & Megahan 1998). The causes of increased peak discharges are controversial, but one of several possible mechanisms is that roads have changed the routing of water from hillslopes to streams (Montgomery 1994; Wemple et al. 1996).

We hypothesize that road network effects on flood peaks and debris flows modify patch dynamics in stream and riparian networks. Herein, we outline how road networks interact with stream networks at the landscape scale and, based on examples from recent and current research, illustrate how these interactions might affect biological and ecological processes in stream and riparian systems. Our approach produced a distinctly different picture of the spatial distribution of ecological responses to road networks than that of the road zone-of-influence approach used for assessing effects on terrestrial ecosystems. We sought to present a conceptual framework that is relevant for ecologists and conservation biologists in the process of assessing current ecosystem conditions and planning landscape-scale restoration activities. We hope that this framework will encourage scientists from many disciplines to work toward spatially explicit studies of road effects on whole stream networks.

Conceptual Model of Interactions between Road and Stream Networks

Our conceptual model is a series of premises. Landscapes contain patchwork and network structures defined by vegetation, soil, and other properties reflecting landform evolution, natural disturbances, and land management (Swanson et al. 1997). Patches consist of vegetation of various types or histories of disturbance by natural or management processes. We focused on two types of networks: natural physical networks, including streams, riparian zones, and ridges, and artificial networks, or roads (Fig. 1).

Flows of matter (water, mass movements, sediment, organisms) and energy follow gravitational flowpaths down hillslopes to channels and along channels in the stream network. Although other materials and transport processes (e.g., movement of suspended load, bedload, and coarse woody debris) might be considered, we focused on flood peaks and debris flows because they are best known and they illustrate many of the principles of interactions between road and stream networks in a landscape.

The stream drainage network is ordered: flows from smaller segments coalesce in successively larger segments. The road network consists of segments and junc-

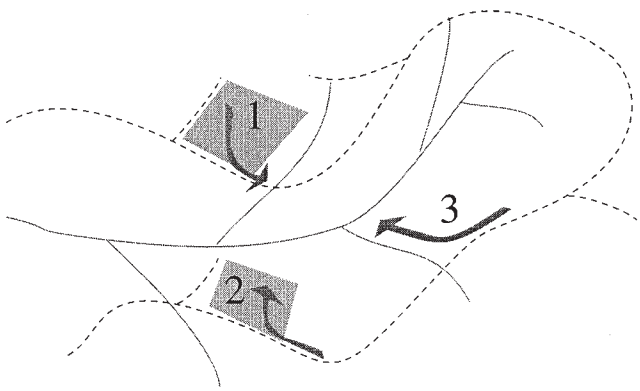

Figure 1. Three types of interactions may occur in a landscape among patches (gray polygons), a road network (dashed line), and a stream network (solid line): (1) patch to road, (2) road to patch, and (3) road to stream. In steep, forested mountain landscapes, patches may be stands of younger vegetation created by a natural disturbance such as wildfire or windthrow or by a human disturbance such as forest harvest.

tions and may be ordered in the sense that spur or dead-end roads sprout from trunk roads; usage intensity is highest and most constant along trunks and lowest and more episodic along spurs (Fig. 1). Some processes are affected by traffic levels (e.g., production of fine sediment, Reid & Dunne 1984), whereas others may not be affected by traffic (e.g., mass movements).

Stream and road networks are similar in five respects: they occupy a small portion of the landscape (commonly only a small percentage of total area), they are widely distributed, and they are "designed" to transport material and energy across a landscape. Stream and road networks also have a high edge length per unit area, hence, opportunity for interaction with neighboring patches. Also, streams and roads commonly occurs at similar densities in mesic or wet-climate mountain landscapes where logging has occurred (Wemple et al. 1996). Road and stream networks differ in that streams flow downslope, whereas roads cross steep slopes (Fig. 2), and roads themselves are not channels, although they often include a ditch that may function as a channel.

Road location in the landscape, specifically hillslope position, strongly influences the type and frequency of interactions between roads and streams (Fig. 2). Roads near ridges have little direct interaction with streams (Montgomery 1994), but roads often cross small tributary streams at perpendicular angles in midslopes and lower slopes, and they commonly are parallel to main stream segments along valley floors (Fig. 2). Consequently, road-stream crossings may be concentrated in middle and lower hillslope positions.

This arrangement of roads relative to stream networks and gravitational flowpaths sets up certain definable geometric interactions involving flows of water and sediment. Energy, organisms, and material may move between patches and network segments or between road segments and stream segments (Fig. 1). Many types of interactions can occur (Fig. 3). A given road segment may act as a barrier, a net source, a net sink, or a corridor relative to flows of water and/or sediment.

Complex combinations of interactions can occur between road segments and flows of water (Fig. 4) or sediment (Fig. 5). Roads may act as corridors for flows of water on road surfaces (A and B, Fig. 4) or in roadside ditches (C, Fig. 4) and as sources of water to stream networks through culverts (D, Fig. 4) or gullies (E, Fig. 4) (Wemple et al. 1996). Roads also may act as sinks for sediment, intercepting slides (A, Fig. 5), as sources of slides (B, Fig. 5), or as corridors transmitting debris flows in stream channels (C, Fig. 5) (Wemple 1998). Encounters with roads may modify the magnitude and direction of flows of water and debris flows, and water flows may transform into debris flows or vice-versa.

The number or density of road-stream crossings provide a useful point of departure for evaluating interactions between road and stream networks at a landscape scale. Because stream and road drainage densities define the number of road-stream crossings (Fig. 6), they define a framework to examine how road design and topographic relief affect road influences on debris flows,

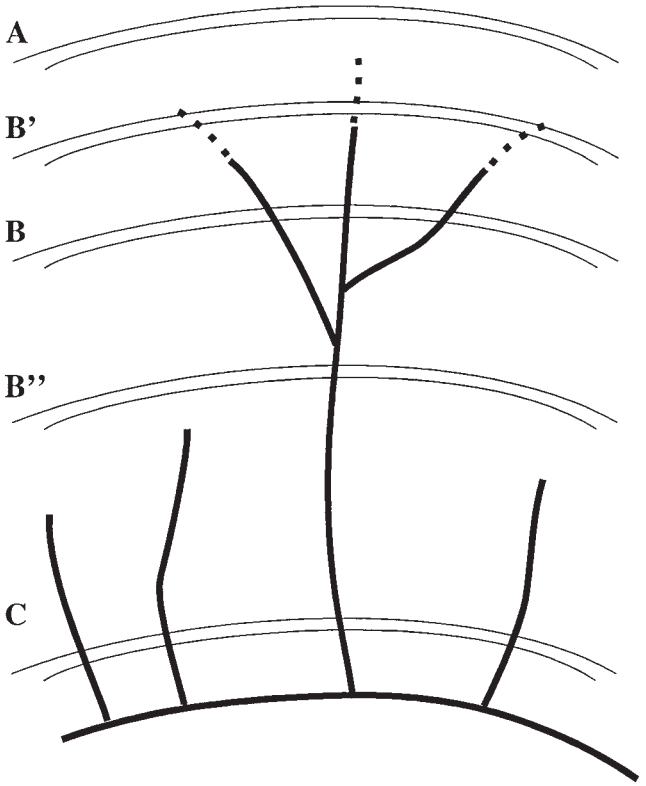

Figure 2. Effects of hillslope position and road design features on road-stream interactions. Roads (double lines) often cross steep tributary streams (dark solid lines) or ephemeral streams (dashed lines) at perpendicular angles in middle and lower hillslope positions (B', B, B"), thus directly affecting peak flows and debris flows. Valley floor roads often run parallel to mainstem streams (C), thus affecting lateral movement of the stream channel and its connectivity to the riparian zone.

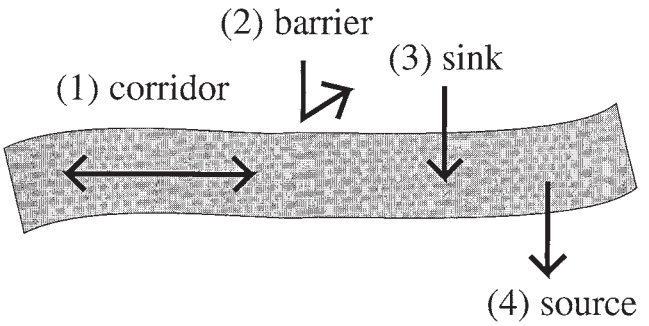

Figure 3. Four basic types of flow interactions with a road segment (shaded).

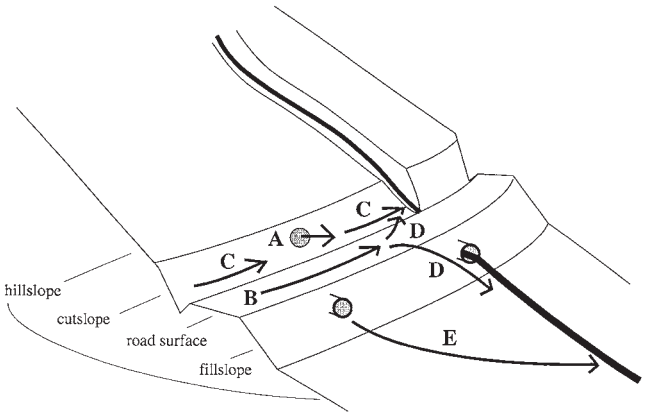

Figure 4. Five types of interactions involving water between a midslope road parallel to contour and a stream (heavy solid line): (A) subsurface flow interception, (B) surface flow on roads, (C) flow routing along ditches to streams, (D) flow along road surface to streams, and (E) flow in gullies to streams.

peak flows, and other measures of the stream network's response to roads.

Roads alter the balance between the intensity of peak flows and the stream and riparian network's resistance to change, whereas they alter the landscape distributions of the starting and stopping points of debris flows. Hence, the two processes may produce somewhat distinct patterns of affected stream network lengths. Systemic, high-severity hydrologic processes such as extreme flood peaks produce a set of disturbance patches controlled by site-specific patterns of resistance to change within the stream network. Road network interactions intensify and redistribute flood energy, thereby producing additional disturbance patches. This pattern of patches

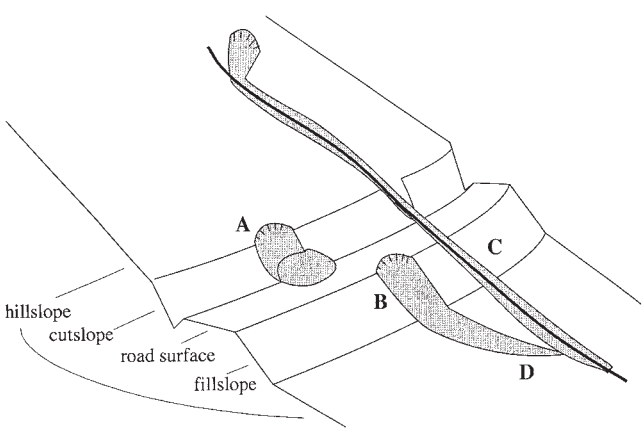

Figure 5. Types of interactions involving debris flows between a midslope road parallel to contour and a stream (heavy solid line): (A) cutslope slides, (B) fillslope slides, (C) debris flows that pass roads, and (D) fillslope slides that become debris flows.

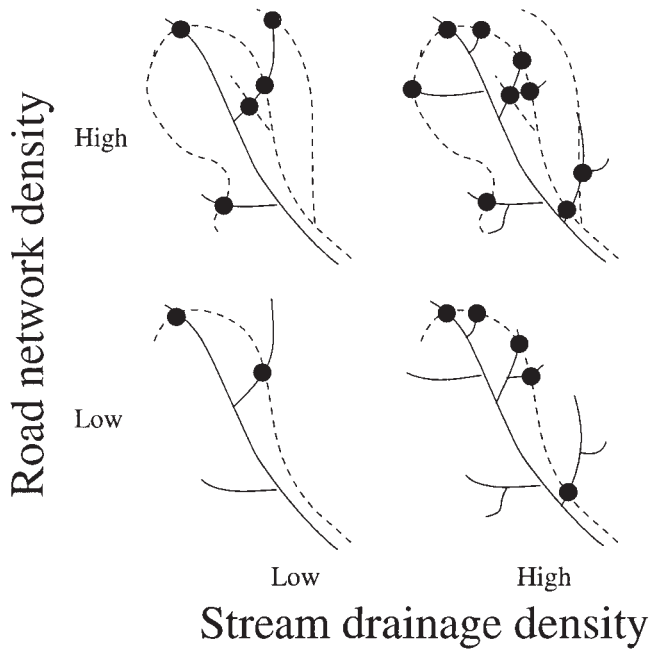

Figure 6. Effects of increasing drainage densities of the road network (dashed line) and the stream network (solid line) on the number of road-stream crossings (black dots) in a landscape.

represents the stream segments downstream of high densities of road-stream crossings where flood energy may disturb the riparian zone (Fig. 7); the actual pattern of flood disturbance patches also will be controlled by factors such as valley floor width, the age and type of vegetation, and the amount of wood and sediment.

On the other hand, localized, high-severity geomorphic processes such as debris flows produce a set of disturbance patches of discrete length extending from initiation sites that may be unaffected by roads. Road network interactions produce additional patches downstream from road-stream crossings where debris flows commonly are initiated (e.g., Swanson et al. 1998; Fig. 8). This pattern of scattered linear patches represents the stream segments where natural debris flows and those associated with roads expend large amounts of energy, scouring the stream bed and removing riparian vegetation, sediment, and wood. Many debris flow tracks end in piles of large wood and boulders deposited by the debris flow; in some cases, roads can stop debris flows, shortening their tracks.

Evidence from Andrews Forest, Oregon

We examined our conceptual model of interactions between road and stream networks based on a number of studies in the H. J. Andrews Experimental Forest, Oregon. The Andrews Forest, located on the western slope

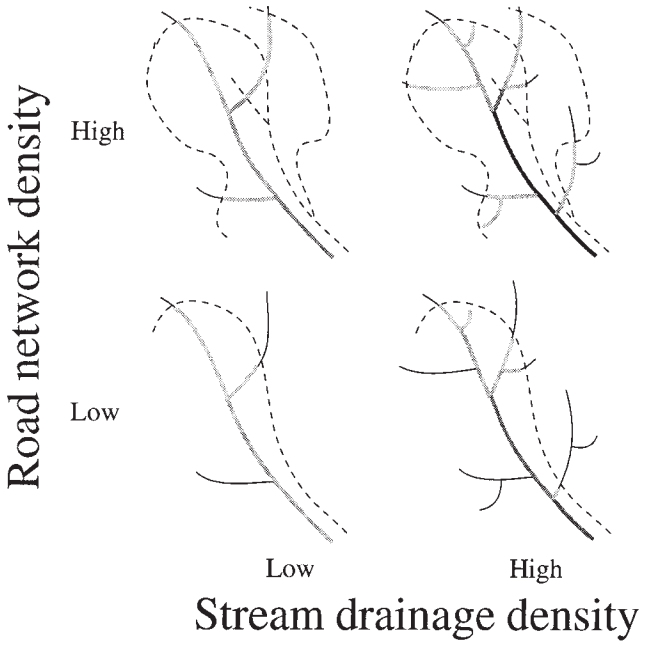

Figure 7. Spatial pattern of peak-flow disturbance patches (greater effect in darker shaded tones) created in a stream network below crossings of the road network (dashed lines) and stream network (solid or gray lines). Higher road and stream drainage densities increase the stream network length with high potential for road-related disturbances. The diagram illustrates a situation in which all road-stream crossings have equal and additive influences on peak flows and all stream segments respond equally. In a real landscape, the actual spatial pattern of stream network susceptibility to road effects on peak flows would be more patchy.

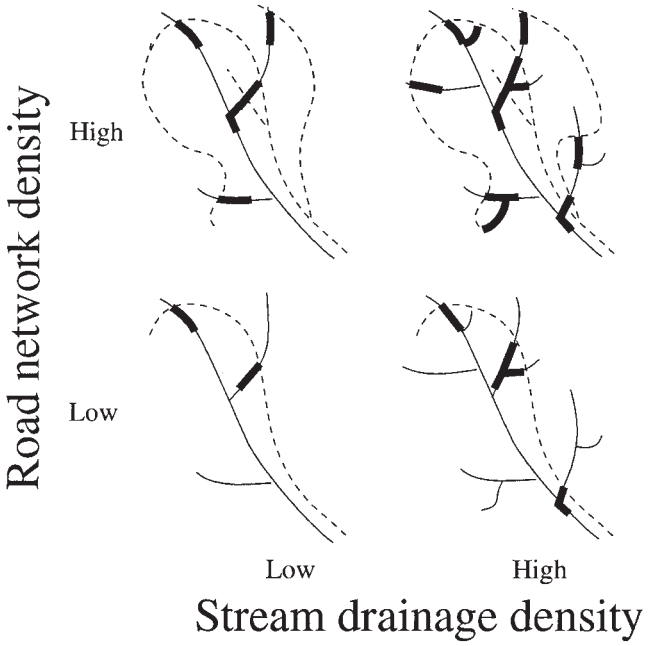

Figure 8. Spatial pattern of debris flow disturbance patches (heavy solid lines) created in a stream network below crossings of the road network (dashed lines) and stream network (thin solid lines). Higher road and stream drainage densities produce larger affected percentages of the stream network. The zones of primary disturbance by debris flows are emphasized, but areas downstream of these patches also may be disturbed. The effect of road-stream crossings in real landscapes is overstated because not every road-stream crossing generates debris flows. Debris flows also occur in the absence of roads, creating additional patches not shown here.

of the Cascade Range in Oregon, has a 50-year history of research on biophysical processes (McKee 1998). The Andrews Forest comprises one drainage basin with steep slopes on highly weathered volcanic substrates. Vegetation cover is mostly old-growth Douglas-fir (*Pseudotsuga menziesii*) forest. Twenty-five percent of the landscape has been harvested and converted to Douglas-fir plantations since 1950. The basin has a relatively high density of forest roads (approximately 2 km/km^2), most of which were constructed in the 1950s and 1960s (Wemple et al. 1996). We examined studies on peak flows and debris flows, evaluating the major forms of evidence of interactions between road and stream networks, the nature of the mechanisms involving roads, and the direction, magnitude, timing and locations of effects on stream channels.

Peak Flows

Three forms of evidence support the assertion that the road network is significantly hydrologically connected to the stream network in the Andrews Forest. First, in small experimental basins, partial logging (25% of basins) with roads appears to have increased large flood peaks (those that occur annually or less often) to the same or greater extent and for longer periods than 100% forest harvest (Jones & Grant 1996; Thomas & Megahan 1998; J. A. Jones, unpublished data). This implies that roads can affect the manner in which incoming precipitation is routed through a basin to produce a flood (Jones & Grant 1996). Second, surveys of road drainage systems indicate that significant portions of the road network have the potential to act as extensions of the stream drainage network (Wemple et al. 1996). Third, Wemple (1998) quantified the amounts of water carried by road segments and showed that this water could be delivered to the stream network to coincide with the flood peak.

Two mechanisms involving peak flows produce interactions between road and stream networks. The cutbanks of roads collect water flowing slowly down a hillslope below the soil surface. Some segments of the

drainage ditches alongside the roads carry water rapidly and directly to streams or to culverts that concentrate water flow and carve gullies down hillslopes to streams (Wemple et al. 1996; Wemple 1998). Interactions between road and stream networks involving water flow seem to have the potential to synchronize water flow through the basin during a storm event, thus increasing the height of the flood peak (Jones & Grant 1996).

The magnitude of increase in flood peaks attributable to interactions between road and stream networks is difficult to separate from the coincident effects of forest harvest. In small harvested basins in western Oregon where road densities are 1–3 km/km^2, roads may increase the height of the peak by at most a few tens of percentage points for floods occurring annually or less frequently (Jones & Grant 1996; Thomas & Megahan 1998; J. A. Jones, unpublished data). In large basins where forest harvest also is confounded with road construction, the combined effects of forest harvest (<25% of basin areas) and road construction appear to have increased floods that occur annually or less frequently by, at most, 100% over the past 50 years (Jones & Grant 1996; Thomas & Megahan 1998). This increase is small relative to the interannual fluctuations in flood size, but it may represent a shift in the distribution of all floods to higher levels than before road construction and harvest occurred.

Debris Flows

The primary evidence of road and stream network effects on debris flows in the Andrews Forest area is the spatial pattern of debris flow tracks from inventory of 50 years of debris flows and debris slides (Swanson & Dyrness 1975; Snyder 2000; Nakamura et al. 2000). Field observations indicate that debris flows frequently are initiated or augmented by debris slides associated with roads; one out of three first- through third-order stream channels crossed by a road at the midslope position were associated with debris-flow initiation (Snyder 2000).

Two mechanisms involving debris flows produce interactions between road and stream networks. Many forest roads in the Andrews were constructed by excavating part of the hillslope and using this material to support the downhill side of the road ("cut-and-fill" roads). During heavy rain events, many small landslides originate from the downslope side of such road segments (the "fillslope"). When these slides occur close to streams, they often reach the streams and become debris flows (Swanson & Dyrness 1975; Wemple 1998; Nakamura et al. 2000). During heavy rains, debris flows also may be triggered by small landslides from forested hillslopes. A second form of road-stream interaction occurs when one of these debris flows moves down a stream channel, encounters a road, and either carries the road fill material further down the stream or stops on the road (Wemple 1998; Swanson et al., unpublished data).

The major effect of roads on streams produced by debris flows is severe disturbance of the stream channel, including removal or rearrangement of all material in some stream segments and deposits of sediment and wood in others. Debris flow tracks were 14 times more frequent per unit area of road than of undisturbed forest in the Andrews Forest and neighboring Blue River basins (Snyder 2000). Debris flow disturbances to streams occur mainly during extreme floods. The most severe effects occur in small, steep stream segments, but some sediment also may be transported to stream segments downstream of these highly disturbed areas, creating additional though less severe disturbances (Snyder 2000; Johnson et al. 2000; Nakamura et al. 2000.

Biological Implications for Stream Networks

Stream networks in both unroaded and roaded landscapes experience both patchy and pervasive disturbances. A key biological implication of floods and debris flows is that they affect only a few percentage of the total area (Miles & Swanson 1986) but tens of percentage of the stream network (Snyder 2000) in mountainous landscapes. Although roads can increase the frequency and extent of these types of disturbances, several factors make it difficult to isolate the extent of road influence on stream and riparian patch dynamics. Disturbance associated with major floods is extremely varied in severity and intensity in complex stream and riparian systems, even when the overall flood disturbance seems pervasive (Swanson et al. 1998; Johnson et al. 2000; Nakamura et al. 2000). Many studies of hydrologic, geomorphic, and ecological processes in stream networks have been conducted in roaded basins, and few studies have been conducted in large areas without roads. No studies we know of have related riparian or benthic habitat patch dynamics and ecology directly to road network distributions. We outline an approach to such studies, emphasizing areas that need research.

A key ecological implication of hydrologic and geomorphic disturbance patterns is that undisturbed areas may function as refuges from disturbance and sources of colonists in the post-disturbance recovery period (Sedell et al. 1990). The patchy character of flood flow and debris flow disturbances (Johnson et al. 2000; Nakamura et al. 2000) leaves numerous refuges in headwater channels undisturbed by debris flows and in undisturbed portions of mainstem channels. Thus, the network structure of stream and riparian systems contributes to their resilience to flood disturbance, and dispersal from undis-

turbed sites can help speed recovery in disturbed zones. If roads increase the frequency and intensity of flood peaks and debris flows, this may increase the extent of debris flows in small streams and possibly the extent of riparian-zone disturbance along main channels, and it may reduce the extent of refuges. Hence, road-network effects on the spatial pattern of disturbance may influence the rates of survival and recovery of disturbed patches in stream networks, which affects ecosystem resilience.

Observed debris-flow tracks typically disturb stream and riparian areas in only a few tributaries in the upper parts of stream networks (Nakamura et al. 2000) (Figs. 3 & 4). Because many tributaries within basins affected by debris flow do not experience such severe disturbance, they serve as refuges during floods. For example, Hunter (1998) observed low densities of amphibians in debris flow tracks created in the previous winter's flood, but amphibian populations in channels that had not experienced debris flows changed little after the flood.

Extreme flood peaks also typically disturb only some portions of the stream network. Flowing water alone is unlikely to damage riparian vegetation, but when a flood carries floating woody debris, especially batches of "congested wood" (Braudrick et al. 2000), vegetation is likely to be toppled or removed (Johnson et al. 2000). Long, narrow patches of disturbed vegetation and undisturbed habitat are common in unconstrained stream segments (e.g., in wide valley floors). These undisturbed patches provide refuges from flood disturbance arrayed both laterally away from the main channel and longitudinally along the channel (Swanson et al. 1998; Fig. 5).

Although we have separated peak flows from debris flows in this discussion, they are confounded. Flood peaks may initiate debris flows, and they may magnify, redistribute, or mute the disturbances produced by debris flows. Debris flows from tributary channels may enter main channels and interact with flood flows, providing batches of woody debris that serve as tools to produce patches of riparian disturbance (Wondzell & Swanson 1999; Johnson et al. 2000; Nakamura et al. 2000.

Biological responses to a disturbance event may be affected by the hillslope position of road-stream interactions. In the Andrews Forest and vicinity, roads in middle hillslope positions were net sources of sediment to the stream network, whereas valley floor roads were net sinks, and the frequency of erosion and deposition features associated with roads was an order of magnitude higher in valley floors than near ridges (Wemple 1998). Stream segments below midslope roads were more likely to be disturbed by debris flows than similar segments without roads (Snyder 2000). Less disturbance may occur in stream segments downstream of valley floor roads than those downstream from midslope roads (Wemple 1998). Roads constructed on valley floors, however, may limit organisms' access to floodplain and secondary channel areas that might otherwise serve as refuges and may limit dispersal of organisms to recolonize flood-disturbed areas.

Assessing Effects of Roads on Stream Networks

Our observations, hypotheses, and perspectives on interactions of road and stream networks, based on field studies conducted in the Pacific Northwest, have several implications for evaluating roads in the context of research, management, and conservation studies. Basins such as Lookout Creek in the Andrews Forest are heterogeneous; they contain areas of naturally high and low rates of peak flow and debris flow production that may affect distributions of habitat and organisms in time and space. Against this backdrop of natural processes and patterns, we propose that the effects of roads on peak flows and debris flows will be greatest downstream of individual road-stream crossings and downstream of areas of high densities of such crossings. Therefore, a field sampling scheme for detecting the magnitude of various road effects on stream and riparian ecology could involve (1) landscape stratification of inherent stream network susceptibility to floods or debris flows, (2) overlay of road and stream networks and creation of areas with various densities of road-stream crossings, emphasizing midslope road-stream crossings, and (3) designations of expected high- and low-impact stream segments based on numbers of upstream road-stream crossings where sampling of selected biological variables would be conducted. It is critical that such locations be selected and interpreted based on their positions in the whole stream network in order to account for the effects of the spatial arrangement of disturbance patches and refugia.

Further Work

We have not attempted to prove that road-stream interactions involving peak flows and debris flows modify the ecology of stream networks, but rather to set out a framework for understanding how such interactions might occur. Field studies may help test how stream disturbances created by extreme floods are related to road-network effects on peak flows and debris flows.

Although we focused on two processes, peak flows and debris flows, other hydrologic and geomorphic processes are influenced by road-stream interactions. Sediment and wood transport is inherently tied to flood- and debris-flow processes and is modified by roads (Reid 1981; Reid & Dunne 1984; Megahan 1987; Bilby et al. 1989; Wemple 1998; Braudrick & Grant 2000; Braudrick et al. 2000; Johnson et al. 2000). Also, interconnected road and stream networks have other functions, notably an ability to facilitate flows along nongravitational path-

ways. For example, evidence presented in Parendes and Jones (this issue) indicates that propagules of exotic plants may be dispersed along forest roads and hence along the stream network from road-stream crossings. These multiple functions of roads have potentially widespread effects on stream networks and deserve further study.

Acknowledgments

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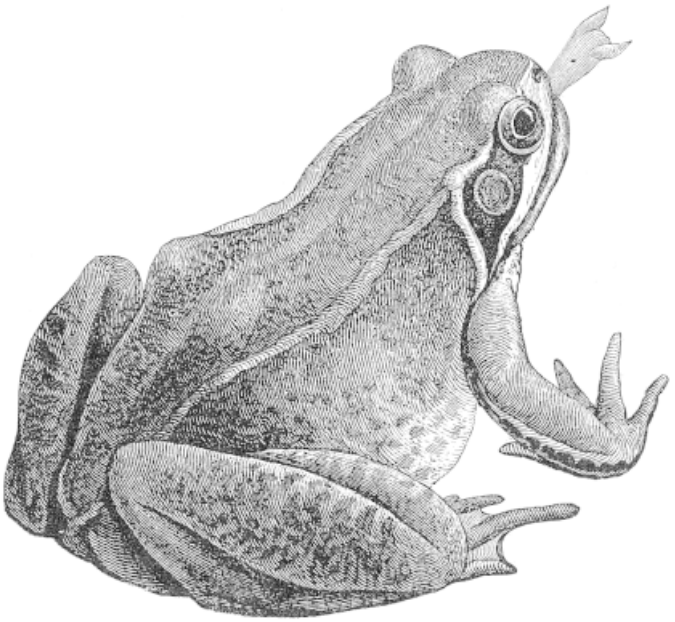

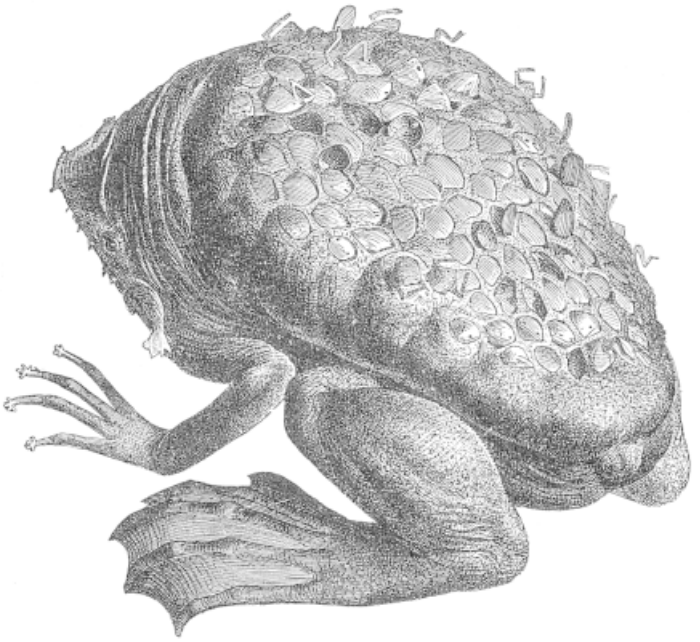

Organized Village of Kake
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Fax 907-785-4902 / www.kake-nsn.gov
(Federally Recognized Tribal Government serving the Kake, Alaska area)

October 10, 2018

Alaska Roadless Rule
U.S.D.A. Forest Service
Alaska Region
Ecosystem Planning and Budget Staff
P.O. Box 21628
Juneau, AK 99802-1628

RE: Organized Village of Kake Comments for Roadless Rule in Alaska

To Whom it may concern,

The Organized Village of Kake (OVK) is the federally recognized Indian Tribe organized under the authority of the Indian Reogranization Acts of 1934 and 1936. OVK is empowered under its Constitution and By-Laws "to aid needy citizens and protect the general welfare and security of the village." One of OVK's highest priorities is to protect the Village's customary and traditional hunting, fishing and gathering areas and uses within the Keex' Kwaan's traditional territory.[1] These lands include national forest lands on Kuiu, Kupreanof, and portions of Baranof & Admiralty Islands, as well as portions of the mainland. OVK would like to engage with the USFS and State of Alaska as a co-manager/cooperater of resources in the traditional Kake, AK area. Many of OVK's citizens are on the ground utlizing all of the areas around Kake and are the first impacted by decision makers 100 miles away in Juneau and 3,000+ miles away in Washington D.C.

On August 2, 2018, in response to the State of Alaska's petition for a full exemption from the 2001 Roadless Area Conservation Rule (Roadless Rule), the Forest Service signed a Memorandum of Understanding with the State of Alaska to develop an Alaska state-specific roadless rule to address the management of inventoried roadless areas on the Tongass National Forest in Southeast Alaska. The U.S. Department of Agriculure announced on August 30, 2018 its intent to prepare an environmental impact statement (EIS) and public rulemaking process to According to the Notice of Intent, the State of Alaska will participate as a cooperating agency in the preparation of the EIS and "Federally recognized Tribes within the Tongass National Forest have been invited to particpate as a cooperating agency." The notice further gave notice of eleven public meetings planned in Southeast Alaska, incuding Kake on September 26, 2018 (Postponed to Oct. 10, 2018).

Pursuant to Executive Order 13175, Departmental Regulation No. 1350-002, and Forest Service Manual (FSM), the United States Forest Service has adopted official policy regarding American Indian and Alaska Native relations. Pursuant to FSM 1563.02, paragraph 4, agency

[1] Goldschmidt & Haas (1946). A map of the traditional territory of the Kake Tlingit prepared by Goldschmidt and Haas is attached, for your information.

American Indian and Alaska Native relations. Pursuant to FSM 1563.02, paragraph 4, agency officials are to "[s]upport the aspirations of the UN Declaration on the Rights of Indigenous Peoples." Specifically, this means "that agency officials should consult with indigenous people – the duly elected officials of federally recognized tribes and the traditional holders of Indian religions, knowledge, and practices – early in their decision-making processes." To further this objective, it is the policy of the Forest Service that "Indian tribes will be provided the opportunity for timely and meaningful government-to-government consultation regarding actions which may have tribal implications." *See* FSM 1563.03. Such consultation requires the agency to "[c]ollaboratively involve Indian tribes, as early as possible, in the development of regulatory and management policies, resource and land management plans, study plans and actions, and Federal undertakings that may have tribal implications." *Id.* at 3.b.

The U.S.D.A. and Forest Service entered into the MOU with the State of Alaska and issued the NOI for preparation of an EIS for an Alaska-specific roadless rule without any consulting or collaboration with OVK, in violation of policies under Executive Order 13175, Departmental Regulation No. 1350-002, and the Forest Service Manual. OVK strongly objects to the agency's utter failure to consult with OVK prior to responding to the State of Alaska's petition and initiating preparation of an EIS to support the rulemaking process. The belated invitation to the Tribe to participate as a cooperating agency, and holding a scoping hearing in Kake, cannot compensate for the agency's abject failure to consult and collaborate with the Tribe before proceeding with this Alaska-specific rulemaking – particularly when the proposed rulemaking has such grave and drastic tribal implications for the many tribal citizens who rely on these lands. Likewise, the State of Alaska's establishment the Alaska Roadless Rule Citizen Advisory Committee, which will include at least one member representing a federally recognized Tribe, will not address our concerns; every tribe should be represented on the committee. First, it appears that this committee by design will not assure fair and balanced representation of both development and non-development interests. Secondly, the proposed schedule for the committee providing recommendations to the Governor and State Forester elevates satisfying the State's hurried and arbitrary timeline above the interests of any other stakeholders in this process.

OVK is concerned that the Forest Service will delay revising the Tongass Land Management Plan, (TLMP) and amend it to authorize logging in roadless areas on a project-by-project basis. In such circumstances, it is likely the agency will tier to the analysis contained in any EIS prepared for this rulemaking. Given the agency must consult and coordinate forest planning on the Tongass with Alaska Native Tribes (36 C.F.R. 291.4), we are gravely concerned that the agency's failure to consult and collaborate adequately with the Tribe on this Alaska-specific rule will impair the agency's performance of its responsibility to consult and coordinate with the Tribe regarding forest planning. Both outcomes impair the Tribe's responsibility to "protect the general welfare and security of the village." As OVK listens to the public comment at other community meetings a large majority of the Alaska citizens are wanting the roadless rule intact and not changed; in fact, more protections are being asked for. In this world of changing climate, the State of Alaska should preserve what is left rather than loosening the regulations to have more development on pristine Tongass roadless areas.

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is attached, for your information.

In conclusion, OVK would like to be at the table while decisions are being made on an Alaska-specific Roadless Rule. OVK would like to engage with the USFS and State of Alaska to guide the projects and activity in the traditional Kake area, from increasing some protections in important cultural areas, to lessening regulations in other areas to promote a sustainable economy. All of the aforementioned decisions should be driven by the communities that utilize that area.

Gunalcheesh,

Joel Jackson pres.

Joel Jackson
President

Cc: Petersburg District Ranger David Zimmerman, dlzimmerman@fs.fed.us
Acting Alaska Regional Forester David E. Schmid, dschmid@fs.fed.us
USDA Forest Service Interim Chief Vicki Christiansen, vcchristiansen@fs.fed.us

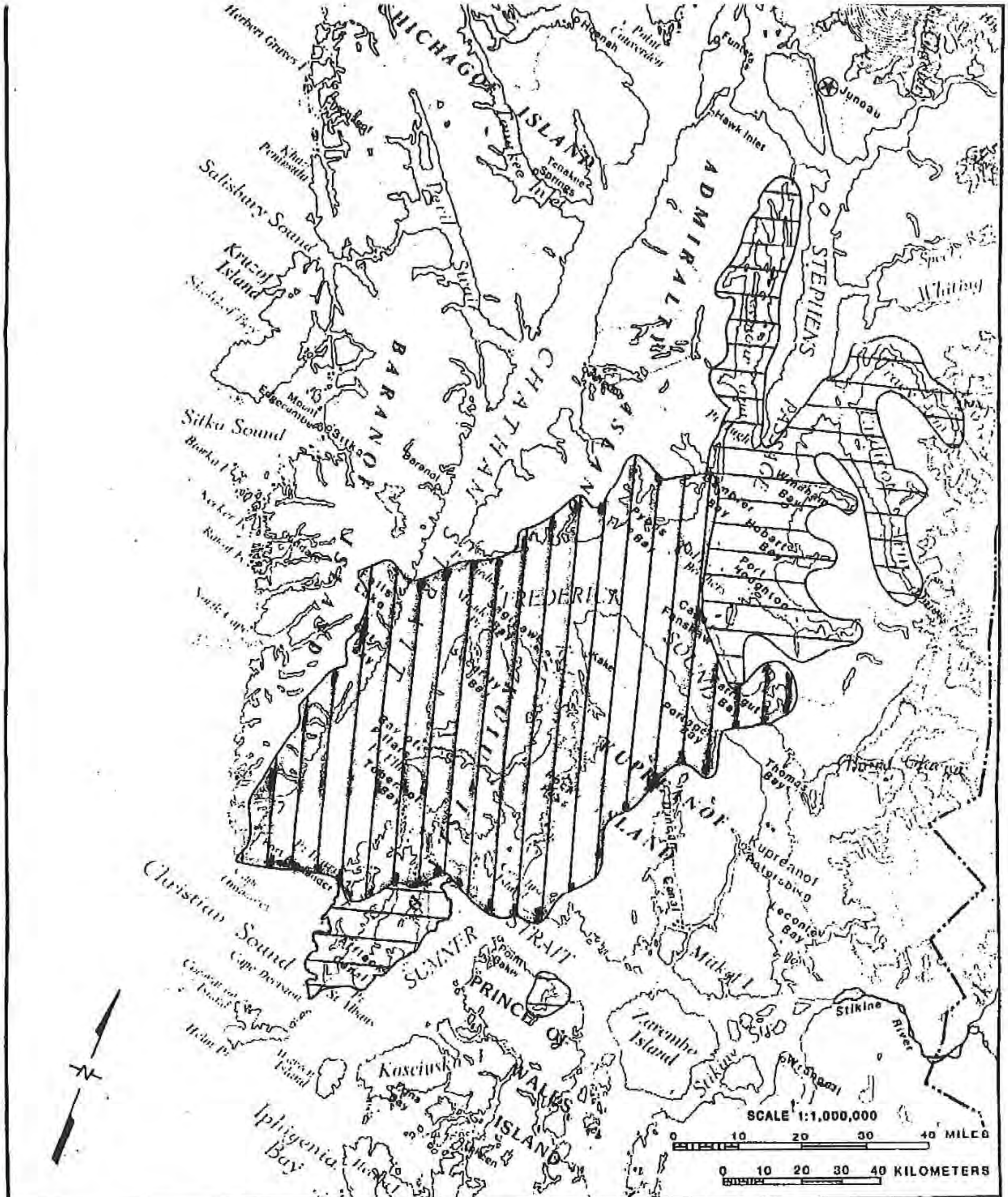
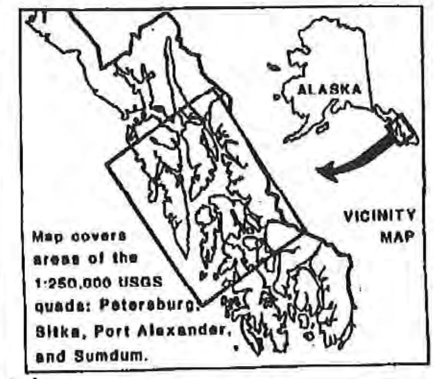


Figure 15. **Traditional Territory of the Kake Tlingit, circa 1943.**

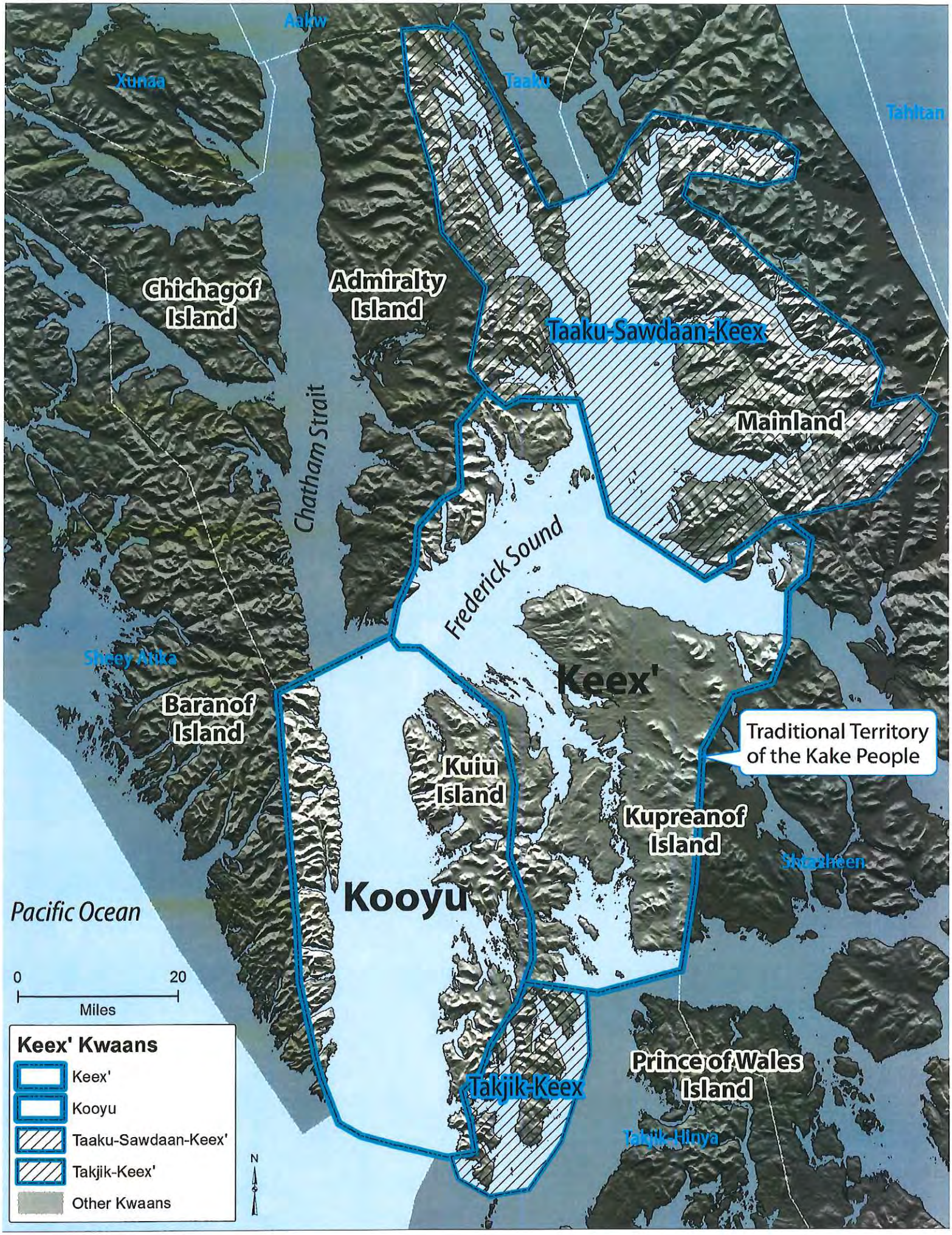


Exclusive Claim Area

Joint Claim Area

SOURCE: Goldschmidt, W.A., and T.H. Haas 1946, Possessory Rights of the Natives of Southeast Alaska and Department of Interior 1944, Hearings on Claims of the Towns of Hydaburg, Klawock, and Kake, Alaska

STATE OF ALASKA
Department of Fish and Game
Subsistence Division


Aakw
Xunaa
Taaku
Tahltan
Chichagof Island
Admiralty Island
Taaku-Sawdaan-Keex
Mainland
Chatham Strait
Frederick Sound
Sheey-Atika
Keex'
Baranof Island
Traditional Territory of the Kake People
Kuiu Island
Kupreanof Island
Shtaxheen
Kooyu
Pacific Ocean
0
20
Miles
Keex' Kwaans
Keex'
Kooyu
Taaku-Sawdaan-Keex'
Takjik-Keex'
Other Kwaans
Takjik-Keex
Prince of Wales Island
Takjik-Hinya
N

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(Federally Recognized Tribal Government serving the Kake, Alaska area)

Resolution No. 2018-24: Continued Tribal Support for Application of National Roadless Rule on the Tongass National Forest

WHEREAS, the Organized Village of Kake (hereinafter OVK) is a federally recognized Indian Tribe under federal law and is empowered under its *Constitution & By-Laws* to execute agreements and contracts with the United States to benefit its members; and,

WHEREAS, OVK is further defined as an Indian Tribe in the Indian Self-determination and Education Assistance Act, PL 93-638 and as such is entitled to contract with the Federal Government for the operation of any federal programs, services, activities or functions serving its member; and,

WHEREAS, our traditional territory includes lands on Kupreanof, Kuiu, Eastern Baranof, and southern Admiralty Islands, and along the mainland, including Port Houghton and as far as Taku River south to Port Houghton; and

WHEREAS, protection of our inherent right to harvest and use our traditional and customary foods requires careful cultural stewardship and protection of our environmental and natural resources; and

WHEREAS, our care of the lands now classified as "inventoried roadless areas" (IRA) and within the Tongass National Forest stretches for millennia; and

WHEREAS, these lands not only provide our people with food, they essentially define who we are and where we come from; and

WHEREAS, inventoried roadless areas protect healthy watersheds that ensure a clean drinking water supply for our Tribal citizens

WHEREAS, inventoried roadless areas contain many sites sacred to Tribal citizens and other Alaska Natives who use these roadless areas for spiritual and religious practices and other customary uses and activities; and

WHEREAS, inventoried roadless areas conserve natural diversity, serve as a bulwark against the spread of invasive species; and

WHEREAS, inventoried roadless areas help ensure the continued protection of indigenous fish and wildlife habitat as it relates to our spiritual, social, nutritional, and ecological values; and

WHEREAS, given Southeast Alaska's cool wet weather, the amount of stored carbon in our intact old-growth forest and soils, the Tongass National Forest represents one of the highest carbon stores in the world and the conservation of intact inventoried roadless areas

on the Tongass is essential for maintaining America's resilience and slowing down climate change throughout the world; and

WHEREAS, the Roadless Rule prevents the disturbance of soils and wasteful construction of damaging roads in inventoried roadless areas; and

WHEREAS, according to the State of Alaska's own economic experts, Tongass timber is uncompetitive because of permanent and fundamental changes in global timber markets, high labor costs, distance from markets, and less expensive substitutes; and

WHEREAS, the Tongass timber industry represents less than one percent of today's jobs and earnings in Southeast Alaska; and

WHEREAS, there are over 5,000 miles of roads already crisscrossing the Tongass National Forest, fragmenting valuable wildlife habitat, threatening salmon by blocking fish passage, and serving as the primary source of sediment into fish streams; and

WHEREAS, spending millions of taxpayer dollars to build roads in inventoried Tongass roadless areas makes no economic sense, particularly given the agency's enormous road maintenance backlog; and

WHEREAS, at hearings held across Southeast Alaska in 2000 on the proposed roadless rule, nearly 60 percent of the Southeast Alaskans who spoke at the hearings supported including the Tongass National Forest in the final roadless rule, and has only grown to upward of 80 percent to date; and

WHEREAS, after the hearing held in Ketchikan during the summer of 2002 on the draft supplemental environmental impact prepared to evaluate recommendations for designating additional inventoried roadless areas on the Tongass as Wilderness, the Ketchikan Daily News reported that roughly 85 percent of the public who testified supported more Wilderness;

WHEREAS, the State of Alaska petitioned the United States Department of Agriculture (USDA) to exempt Tongass inventoried roadless areas from the Roadless Rule on January 19, 2018;

WHEREAS, for all the above reasons, the State's petition severely mischaracterizes the actual extent and impacts of the Roadless Rule on Southeast Alaska; and

WHEREAS, the State's petition ignores the fact that the USDA narrowly tailored the Roadless Rule to limit only two activities in roadless areas, road construction and commercial logging; and

WHEREAS, the State of Alaska's petition ignores the Rule's established exceptions, including Federal Aid Highway projects connecting communities, access to mining claims, and logging incidental to otherwise permitted activities, including utility corridors and hydropower projects; and

WHEREAS, on August 2, 2018, the Forest Service signed a Memorandum of Understanding (MOU) with the State of Alaska to develop an Alaska-specific roadless rule that addresses management of inventoried roadless areas on the Tongass National Forest; and

WHEREAS, three days before the MOU was signed and six months after the State filed its petition, the Forest Service informed OVK by a letter dated 30 July 2018 that the U.S. Secretary of Agriculture Perdue and State of Alaska Governor Walker had reached an agreement to prepare an Alaska-specific rule that would replace the Roadless Rule and "provid[e] for activities needed to further the State of Alaska's economic development while conserving roadless areas for future generations;" and

WHEREAS, the July 30th letter served as an invitation from Acting Regional Forester David E. Schmid to a "Tribal Leader" inviting "government-to-government consultation in advance of a formal public comment period and an opportunity for your Tribe to participate as a cooperating agency" because of our "expertise on subsistence and potential impacts to specific communities within Alaska" during preparation of an environmental impact statement (EIS) to evaluate the proposed Alaska-specific roadless rule for the Tongass National Forest, and other alternative; and.

WHEREAS, the U.S. Department of Agriculture, which includes the Forest Service, published a Notice of Intent (NOI) published on August 30, 2018 announcing its intent to prepare an environmental impact statement (EIS) and initiate a public rulemaking process; and

WHEREAS, the joint announcement issued by the Forest Service when the MOU was signed promises to leave unaffected Tongass lands designated Wilderness by Congress, no mention is made of the fate of nearly 900,000 acres of Legislated LUD II lands designated for perpetual protection from logging and roadbuilding by Congress in the 1990 Tongass Timber Reform Act and the 2014 Sealaska Lands Bill; and

WHEREAS, Kuiu Island and the surrounding smaller islands are important to the residents of Kake, especially the coastal areas near Kake. Areas most often associated with higher values include the Keku Islands, Kadake Bay and Creek, Port Camden, Rocky Pass, and the East Kuiu Roadless Area on the south and east side of Kuiu Island in addition to all of Kupreanof;

WHEREAS, any rule that weakens or eliminates Roadless Rule protections within our traditional territory in what became Inventoried Roadless Areas of the Tongass National Forest will substantially affect the existing 2016 Tongass Land Management Plan Amendment; and

WHEREAS, the 2016 Plan Amendment excluded all roadless areas from the available timber base, the agency's failure to consult and coordinate forest planning with OVK will impair the Tribe's ability to fulfill its responsibility to "protect the general welfare and security" of Tribal citizens; and.

WHEREAS, pursuant to Executive Order 13175, Departmental Regulation No. 1350-002, and Forest Service Manual (FSM), the United States Forest Service adopted an official policy (FSM 1563.02, paragraph 4) to "[s]upport the aspirations of the UN Declaration on the Rights of Indigenous Peoples." Specifically, this means "that agency officials should consult with indigenous people – the duly elected officials of federally recognized tribes and the traditional holders of Indian religions, knowledge, and practices – early in their decision-making processes;" and

WHEREAS, as provided in FSM 1563.03, it is the policy of the Forest Service that "Indian tribes will be provided the opportunity for timely and meaningful government-to-government consultation regarding actions which may have tribal implications" and such consultation requires the agency to "[c]ollaboratively involve Indian tribes, as early as possible, in the development of regulatory and management policies, resource and land management plans, study plans and actions, and Federal undertakings that may have tribal implications;" and

WHEREAS, the USDA and Forest Service entered into an MOU with the State of Alaska and issued the NOI for preparation of an EIS for an Alaska-specific roadless rule without prior consultation or collaboration with OVK; and

WHEREAS, the Forest Service has not explained adequately why it failed to fulfill its responsibilities to consult with the Tribe; and

WHEREAS, the State of Alaska continues to resist all efforts to develop and work in a government to government relationship with the Tribes and never consulted with the OVS before filing its petition with the USDA; and

WHEREAS, Governor Walker issued Administrative Order 299, establishing the Alaska Roadless Rule Citizen Advisory Committee (CAC) on September 5, 2018; and

WHEREAS, Alaska Governor Walker appointed 13 Alaskans to the CAC, including the Alaska State Forester, to advise the State of Alaska on the future management of inventoried roadless area in the Tongass National Forest; and

WHEREAS, the Governor appointed a single Alaska Native to represent all Tribal perspectives for the seventeen federally-recognized Tribes of Alaska Natives in Southeast Alaska on the CAC, a gigantic and unrealistic burden for one person; and

WHEREAS, the only other Alaska Native on the CAC represents Sealaska Corporation; and

WHEREAS, Sealaska is an Alaska Native for-profit Corporation established under the Alaska Native Claims Settlement Act -- not a Tribe; and

THEREFORE BE IT RESOLVED, OVK strongly supports lasting protection for all inventoried roadless areas within OVK's traditional territory now within the Tongass National Forest as provided for in the Roadless Rule; and

THEREFORE BE IT FURTHER RESOLVED, given the serious and long lasting Tribal implications from any reduction in current Roadless Rule protections, we strongly object to the Forest Service's failure to consult with OVK before deciding to grant the State of Alaska's petition and begin a review under the National Environmental Policy Act and public rulemaking process;

THEREFORE BE IT FURTHER RESOLVED, the only changes to the Roadless Rule that OVK can support is an update to the inventory used to define inventoried roadless areas subject to the Rule on the Tongass to include approximately 350,000 acres excluded from the 1995 inventory used for developing the 2001 Roadless Rule because the agency assumed approved logging development would occur – when it did not;

BE IT FINALLY RESOLVED, the Forest Service must also initiate consultation, coordination, and accommodation of Tribal interests in any changes to TLMP connected with this rulemaking process.

CERTIFICATION

This resolution was duly adopted at an IRA Council meeting held this _____ day of _____, 2018 by a quorum of _____ (includes president as non-voting chairperson except in case of tie vote) with _____ yes votes, _____ no votes, and _____ abstaining.

Joel Jackson pres.
Joel Jackson, President

Patti Landy vice
Attested by

Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests

Heather Keith[1], Brendan G. Mackey, and David B. Lindenmayer

The Fenner School of Environment and Society, Australian National University, Canberra, ACT 0200, Australia

Communicated by Gene E. Likens, Cary Institute of Ecosystem Studies, Millbrook, NY, March 9, 2009 (received for review July 14, 2008)

From analysis of published global site biomass data (n = 136) from primary forests, we discovered (*i*) the world's highest known total biomass carbon density (living plus dead) of 1,867 tonnes carbon per ha (average value from 13 sites) occurs in Australian temperate moist *Eucalyptus regnans* forests, and (*ii*) average values of the global site biomass data were higher for sampled temperate moist forests (n = 44) than for sampled tropical (n = 36) and boreal (n = 52) forests (n is number of sites per forest biome). Spatially averaged Intergovernmental Panel on Climate Change biome default values are lower than our average site values for temperate moist forests, because the temperate biome contains a diversity of forest ecosystem types that support a range of mature carbon stocks or have a long land-use history with reduced carbon stocks. We describe a framework for identifying forests important for carbon storage based on the factors that account for high biomass carbon densities, including (*i*) relatively cool temperatures and moderately high precipitation producing rates of fast growth but slow decomposition, and (*ii*) older forests that are often multiaged and multilayered and have experienced minimal human disturbance. Our results are relevant to negotiations under the United Nations Framework Convention on Climate Change regarding forest conservation, management, and restoration. Conserving forests with large stocks of biomass from deforestation and degradation avoids significant carbon emissions to the atmosphere, irrespective of the source country, and should be among allowable mitigation activities. Similarly, management that allows restoration of a forest's carbon sequestration potential also should be recognized.

Eucalyptus regnans | climate mitigation | primary forest | deforestation and degradation | temperate moist forest biome

Deforestation currently accounts for ≈18% of global carbon emissions and is the third largest source of emissions (1). Reducing emissions from deforestation and degradation (REDD) is now recognized as a critical component of climate change mitigation (2). A good understanding of the carbon dynamics of forests (3) is therefore important, particularly about how carbon stocks vary in relation to environmental conditions and human land-use activities. Average values of biomass carbon densities for the major forest biomes (4) are used as inputs to climate-carbon models, estimating regional and national carbon accounts, and informing policy debates (5). However, for many purposes it is important to know the spatial distribution of biomass carbon within biomes (6) and the effects of human land-use activities on forest condition and resulting carbon stocks (refs. 3 and 7 and www.fao.org/forestry/site/10368/en).

Primarily because of Kyoto Protocol rules (ref. 8; http://unfccc.int/resource/docs/convkp/kpeng.pdf), interest in carbon accounting has been focused on modified natural forests and plantation forests. It has been argued that primary forests, especially very old forests, are unimportant in addressing the climate change problem because (*i*) their carbon exchange is at equilibrium (9, 10), (*ii*) carbon offset investments focus on planting young trees as their rapid growth provides a higher sink capacity than old trees, and/or (*iii*) coverage and hence importance of modified forest is increasing. Recent research findings have countered the first argument for all 3 major forest biomes (namely, tropical, temperate, and boreal forests) and demonstrated that old-growth forests are likely to be functioning as carbon sinks (11–13). The long time it takes new plantings to sequester and store the amount of carbon equivalent to that stored in mature forests counters the second argument (14). The third argument about the unimportance of old forest in addressing climate change relates, in part, to the diminishing extent of primary forest caused by land-use activities (15) and associated depletion of biomass carbon stocks (16). However, significant areas of primary forest remain (17), and depleted carbon stocks in modified forests can be restored.

It is useful to distinguish between the carbon carrying capacity of a forest ecosystem and its current carbon stock. Carbon carrying capacity is the mass of carbon able to be stored in a forest ecosystem under prevailing environmental conditions and natural disturbance regimes, but excluding anthropogenic disturbance (18). It is a landscape-wide metric that provides a baseline against which current carbon stocks (that include anthropogenic disturbance) can be compared. The difference between carbon carrying capacity and current carbon stock allows an estimate of the carbon sequestration potential of an ecosystem and quantifies the amount of carbon lost as a result of past land-use activities.

This study re-evaluates the biomass carbon densities of the world's major forest biomes based on a global synthesis of site data of biomass measurements in forest plots from publicly available peer-reviewed articles and other reputable publications. Site data were selected that (*i*) provided appropriate measurements of biomass and (*ii*) sampled largely mature and older forests to provide an estimate of carbon carrying capacity. The most reliable nondestructive source of biomass carbon data are from field measurements of tree and dead biomass structure at sites that sample a given forest type and condition. These structural measurements are converted to biomass carbon densities by using allometric equations. Standard national forestry inventories contain site data but they are not always publicly available and their suitability for estimating carbon stocks at national and biome-levels has been questioned (5, 6).

We identify those forests with the highest biomass carbon densities and consider the underlying environmental conditions and ecosystem functions that result in high carbon accumulation. These results (*i*) provide a predictive framework for identifying forests with high biomass carbon stocks, (*ii*) help clarify interpretation of average forest biome values such as those published by the Intergovernmental Panel on Climate Change (IPCC), and (*iii*) inform policies about the role of forests in climate change mitigation.

Australian *Eucalyptus regnans* Forests Have the World's Highest Biomass Carbon Density

Evergreen temperate forest dominated by *E. regnans* (F. Muell.) (Mountain Ash) in the moist temperate region of the Central

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Fig. 1. *E. regnans* forest with midstory of *Acacia* and understory of tree ferns. The person in the bottom left corner provides a scale.

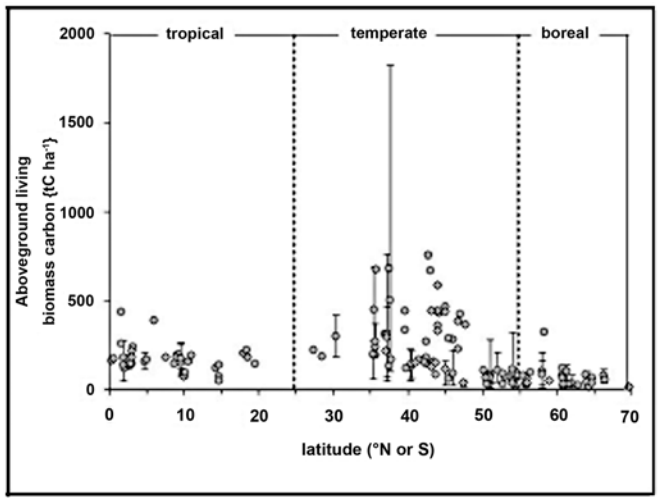

Fig. 2. Global forest site data for above-ground biomass carbon (tC·ha^{-1}) in relation to latitude (north or south). Points are values for individual or average of plots, and bars show the range in values at a site. The O'Shannassy Catchment has a mean of 501 tC·ha^{-1} and ranges from 104 to 1,819 tC·ha^{-1}. The highest biomass carbon occurs in the temperate latitudes.

Highlands of Victoria, southeastern Australia has the highest known biomass carbon density in the world. We found that *E. regnans* forest in the O'Shannassy Catchment of the Central Highlands (53 sites within a 13,000-ha catchment) contains an average of 1,053 tonnes carbon (tC)·ha^{-1} in living above-ground biomass and 1,867 tC·ha^{-1} in living plus dead total biomass in stands with cohorts of trees >100 years old sampled at 13 sites. We examined this catchment in detail because it had been subject to minimal human disturbance, either by Indigenous people or from post-European settlement land use. We compared the biomass carbon density of the *E. regnans* forest with other forest sites globally by using the collated site data (Table S1). No other records of forests have values as high as those we found for *E. regnans*.

Our field measurements and calculations revealed that maximum biomass carbon density for a *E. regnans*-dominated site was 1,819 tC·ha^{-1} in living above-ground biomass and 2,844 tC·ha^{-1} in total biomass from stands with a well-defined structure of overstory and midstory trees (see Fig. 1) consisting of multiple age cohorts with the oldest ≈250+ years (19). There was substantial spatial variability in total biomass carbon density across the sites in the catchment within an ecologically mature forest type, ranging from 262 to 2,844 tC·ha^{-1}. Unexpectedly, we found the highest values were from areas experiencing past partial stand-replacing natural disturbances.

In February 2009, extensive areas of the O'Shannassy Catchment and elsewhere in the Central Highlands of Victoria were burned in a major conflagration. We will be undertaking a major survey of the network of permanent field sites in the catchment (20) to assess changes in postfire carbon stocks. It will be important that these sites are not subject to postfire salvage logging over the coming years to prevent the extensive removal of dead biomass carbon (21).

Some Temperate Moist Forest Types Can Have Higher Biomass Carbon Density Than Both Boreal and Tropical Forests

Average values of the collated global site biomass data from largely mature or primary forests were much higher for the sampled temperate moist forests (n = 44) than they were for the sampled tropical (n = 36) and boreal (n = 52) forests, where n is the number of sites in each forest biome (Table S1) (Fig. 2). The locations of the global site biomass data are shown in Fig. S1. They do not represent all forest types or environmental conditions within a given biome (reflecting the difficulty of finding published field data) and therefore are insufficient to calculate biome spatial averages. We related site values of above-ground living biomass carbon (tC·ha^{-1}) and total biomass carbon (tC·ha^{-1}) to temperature and precipitation (Fig. 3).

Fig. 3 shows that temperate moist forests occurring where temperatures were cool and precipitation was moderately high had the highest biomass carbon stocks. Temperate forests that had particularly high biomass carbon density included those dominated by *Tsuga heterophylla*, *Picea sitchensis*, *Pseudotsuga menziesii*, and *Abies amabilis* in the Pacific Northwest of North America [range in living above-ground biomass of 224−587 tC·ha^{-1} and total biomass of 568–794 tC·ha^{-1} (22–25)]. A synthesis of site data for the Pacific Northwest gave an average for evergreen needle leaf forest of 334 tC·ha^{-1} (26), and this is used as the continental biome value by the IPCC (4). An upper limit of biomass accumulation of 500–700 tC·ha^{-1} in the Pacific Northwest of the United States has been derived from an analysis of global forest data of carbon stocks and net ecosystem productivity in relation to stand age (11, 27). In New Zealand, the highest biomass carbon density reported is for *Agathis australis* [range in living above-ground biomass of 364–672 and total biomass of 400–982 tC·ha^{-1} (28)]; and a synthesis based on forest inventory data gave a mean of 180 tC·ha^{-1} with a range in means for forest classes of 105–215 tC·ha^{-1} (29). In Chile, the highest biomass carbon densities reported are for *Nothofagus*, *Fitzroya*, *Philgerodendron*, and *Laureliopsis* [range in living above-ground biomass 142–439 and total biomass of 326–571 tC ha^{-1} (30–33)].

IPCC Tier-1 Biome Default Values

IPCC biome default values are shown in Table 1 alongside the published global site biomass data (Table S1). The site data were averaged for each biome but they are not equivalent to a spatial average for each biome. The comparison helps identify biomes where site averages differ significantly from default values. The biome-averaged values of the global site biomass carbon data were 2.5–3 times higher than the IPCC biome default values for warm and cool temperate moist forests (Table 1). The IPCC default

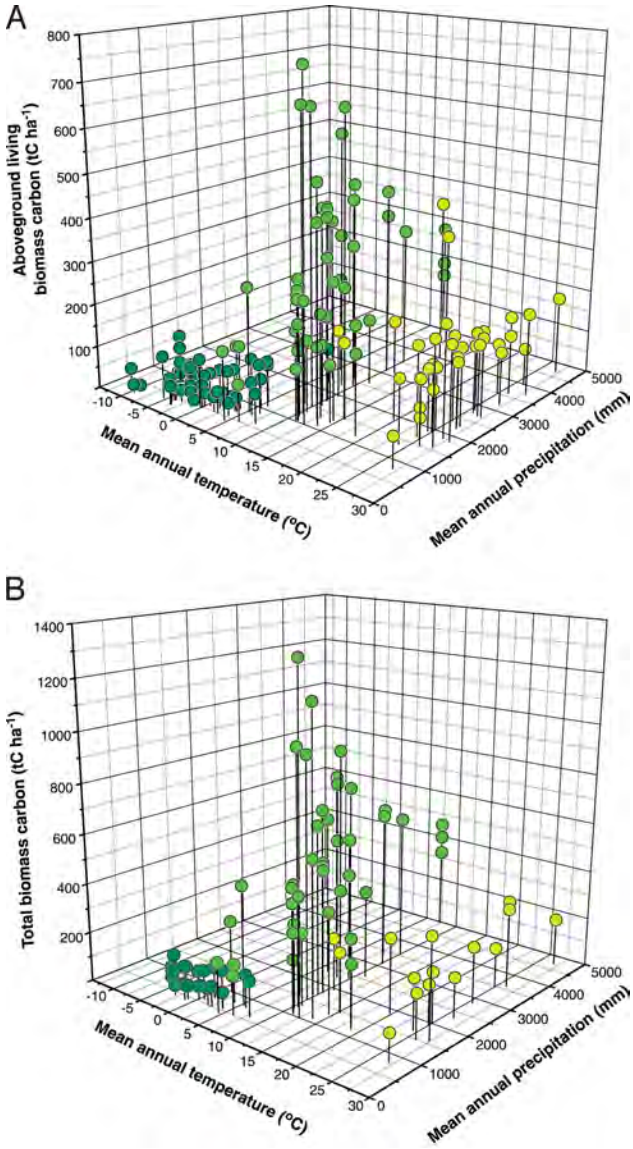

Fig. 3. Global forest site data for above-ground living biomass carbon (tC·ha^{-1}) (*A*) and total biomass carbon (tC·ha^{-1}) (*B*), in relation to mean annual temperature and mean annual precipitation for the site. Site data are shown in relation to their distribution among biomes of boreal (dark green), temperate (midgreen), and tropical (light green) forests. The highest biomass carbon density occurs in cool, moderately wet climates in temperate moist forest biomes. Some sites had values for above-ground living biomass carbon but not dead biomass, so there was no value for total biomass carbon.

values were <1 SD from the averaged site values. Average site data were comparable with IPCC default values for tropical and boreal biomes. However, the IPCC biome default value for tropical moist forest was marginally <1 SD from the averaged site values. Also, the site data for the boreal biome reflected higher above-ground living biomass carbon values but lower below-ground plus dead biomass carbon values compared with the IPCC default values (Table 1).

The differences between the collated global site biomass data and IPCC biome default values for temperate moist forests reflect the diversity of forest ecosystem types considered under the temperate biome category. Biome default values likely under-represent Southern Hemisphere evergreen temperate moist forest types and do not distinguish forest condition caused by land-use history (5). The differences between site biomass data and IPCC default values for boreal forests could reflect the effect of land-use history and fire on carbon stocks at the site level.

Toward a Predictive Framework for High Biomass Carbon Forests

We developed a framework for identifying forests with high biomass carbon stocks based on an understanding of underlying mechanisms and using the *E. regnans* forests as an example. The factors in the framework include (*i*) environmental conditions, (*ii*) life history and morphological characteristics of tree species, and (*iii*) the impacts of natural disturbance such as fire and land-use history. It is the interactions and feedbacks among these factors that influence vegetation community dynamics and ultimately lead to very high carbon densities.

Derivation of Carbon Stocks. Stock of carbon represents the net exchange of carbon fluxes in an ecosystem (net ecosystem exchange). In living biomass, the carbon stock is determined by the balance between the fluxes of carbon gain by photosynthetic assimilation by the foliage [gross ecosystem production (GEP)] and carbon loss by autotrophic respiration, which results in net primary productivity (NPP). In the total ecosystem (living plus dead biomass plus soil), the carbon stock is determined by the balance between the fluxes of carbon gain by NPP and carbon loss by decomposition of dead biomass and heterotrophic respiration. Ecosystem carbon stocks vary because environmental conditions influence the carbon fluxes of photosynthesis, decomposition, and autotrophic and heterotrophic respiration differently (34).

Environmental Conditions. The key climatic variables of precipitation, temperature, and radiation are broadly correlated with vegetation structure and function (35, 36), although such empirical correlations do not necessarily reveal underlying biochemical processes or the dependence of these processes on environmental factors (37). Climatic influences on photosynthesis include effects of (*i*) irradiance and temperature on carboxylation rates, (*ii*) temperature and soil water status on stomatal conductance and thus diffusion of CO_2 from the atmosphere into the intercellular air spaces, and (*iii*) temperature-dependent nitrogen uptake (37). The climatic conditions and relatively fertile soils of the Central Highlands of Victoria favor rapid growth of *E. regnans* (>1 m·yr^{-1} for the first 70 years), and these trees eventually become the world's tallest flowering plant (up to 130 m) (38).

Both dark respiration and maintenance respiration are temperature dependent (37). Soil respiration is correlated with temperature and water availability, although substrate also has an important influence (34). Rates of coarse woody biomass decomposition have been found to decrease with lower temperatures in temperate forests (39) and are also related to wood density, chemistry, and size (40–42).

Climatic conditions that favor higher rates of GEP relative to rates of respiration and decomposition should, other factors being equal, lead to larger biomass carbon stocks. Table 2 gives the average and range in climatic conditions (annual precipitation and temperature) for the global site data from Table S1 and compares estimates of GEP (34) and decomposition rates (*k*) (42). Estimates of the climate conditions and derived variables are also shown for *E. regnans* forests in the Central Highlands of Victoria. Temperate forests are characterized by higher rates of GEP than boreal forests but lower decomposition rates than tropical forests. There is considerable variation evident in rates of carbon fluxes within each forest biome, along with overlap between biomes.

Life History and Morphological Characteristics of Tree Species. *E. regnans* can live for ≈450 years, with stem diameters up to 6 m (38, 43). In our analysis, the stands of *E. regnans* with high values of biomass carbon density were at least 100 years old. *E. regnans* wood density is high (450–550 g·cm^{-3}) (44), so that biomass is greater for a given volume. Limited crown development in *E. regnans* (through crown shyness or reduced crown area caused by abrasion of growing tips by neighboring crowns) and the isolateral leaf form of this

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Table 1. Average published site data (from Table S1) for biomass carbon (tC·ha^{-1}) of each forest biome (mean, standard deviation, and number of sites) and default biomass carbon values (IPCC; refs. 4 and 66)

		Above-ground living biomass carbon, tC·ha^{-1}		Root + dead biomass carbon, tC·ha^{-1}		Total living + dead biomass carbon, tC·ha^{-1}	
Domain	Climate region	Average site data	Biome default value*	Average site data	Biome default value†	Average site data	Biome defaul value
Tropical	Tropical wet	171 (61) n = 18	146	76 (72) n = 7	67	231 (75) n = 7	213
	Tropical moist	179 (96) n = 14	112	55 (66) n = 5	30	248 (100) n = 5	142
	Tropical dry	70 n = 1	73	41 n = 1	32	111 n = 1	105
	Tropical montane	127 (8) n = 3	71	52 (6) n = 3	60	167 (17) n = 3	112
Subtropical	Warm temperate moist	294 (149) n = 26	108	165 (75) n = 20	63	498 (200) n = 20	171
	Warm temperate dry		75		65		140
	Warm temperate montane		69		63		132
Temperate	Cool temperate moist	377 (182) n = 18	155	265 (162) n = 18	78	642 (294) n = 18	233
	Cool temperate dry	176 (102) n = 3	59	102 (77) n = 3	62	278 (173) n = 3	121
	Cool temperate montane	147 n = 1	61		63	153 n = 1	124
Boreal	Boreal moist	64 (28) n = 28	24	37 (16) n =14	75	97 (34) n =14	99
	Boreal dry	59 (36) n = 24	8	25 (12) n = 9	52	84 (39) n = 9	60
	Boreal montane		21		55		76

The site data represent an average and variance of point values whereas the default values represent a spatial average. The site data have been taken from mature and older forests with minimal human land use impact whereas the default values do not distinguish between natural undisturbed forest and regenerating forest nor forest age (unless <20 years). Domain and climate region classification are according to Table 4.5 and defined in Table 3A.5.2 (4).

*Default values are from the IPCC (4). Above-ground biomass from Table 4.7 (4) averaged across continents for each ecological zone. Carbon fraction in above-ground biomass [Table 4.3 (4)].

†Default values are from the IPCC (4, 66). Litter carbon stocks [Table 3.2.1 (66)]. Ratio of below- to above-ground biomass [Table 4.4 (4)]. Dead wood stocks [Table 3.2.2 (66)].

species enable high levels of light to penetrate the forest floor, allowing luxuriant understory layers to grow (45). Eucalypt foliage is evergreen and minimum winter temperatures in the Central Highlands are moderate, so *E. regnans* trees can grow all year. Similarly, evergreen temperate forests of the Pacific Northwest of North America with high biomass have been found to photosynthesize throughout the year (46).

Natural Disturbance Such as Fire. Fire affects vegetation structure and biomass carbon stocks at multiple spatial scales, such as the landscape, stand, and individual tree levels. Fire can kill but not combust all of the material in trees, leading to much of the biomass carbon changing from the living biomass pool to the standing dead and fallen dead biomass pools. The amount of carbon lost from the forest floor and the soil profile may vary depending on ecosystem type, fire regimes, and postdisturbance weather conditions (47). The dead biomass then decays as the stand grows (48). Slow decomposition rates can therefore result in large total carbon stocks of dead biomass and regrowing living biomass. A study of temperate forests along a subalpine elevation gradient in the United States estimated coarse woody debris turnover time to be 580 ± 180 years (39). Large amounts of coarse woody debris biomass are also typical of old-growth forests of the Pacific Northwest of North America (40).

Unlike the majority of eucalypt species, *E. regnans* does not regenerate by epicormic growth or sprouting from lignotubers after a wildfire. Rather, a tree is killed if its canopy is completely scorched by fire. It then sheds seeds that germinate in the postfire ash-bed conditions (49). In the Central Highlands of Victoria, wetter sites on lower slopes and shaded aspects support longer fire intervals and less intense fires, leading to a greater probability of multiaged stands (50). Whether environmentally controlled or the result of stochastic processes, past partial stand-replacing wildfires produce younger cohorts of fast-growing *E. regnans* trees, mixed with an older cohort of living and dead trees, together with rejuvenating the understory of *Acacia* spp. and other tree species (Fig. 1).

Table 2. Comparison of mean and range climatic conditions for boreal, temperate, and tropical forest biomes based on the global site data (Table S1 and Fig. 3)

Condition	Mean annual temperature, ° C	Total annual precipitation, mm	GEP, g CO_2 m^{-2} y^{-1}	k, year^{-1}
Boreal: mean	−0.6	581	822	0.01
Minimum	−10.0	213	382	0.01
Maximum	8.0	2,250	1,228	0.03
Temperate: mean	9.9	1,850	1,318	0.04
Minimum	1.5	404	923	0.02
Maximum	18.9	5,000	1,740	0.08
Tropical: mean	23.6	2,472	1,961	0.12
Minimum	7.2	800	1,190	0.03
Maximum	27.4	4,700	2,140	0.17
E. regnans: mean	11.1	1,280	1,374	0.04
Minimum	7.0	661	1,181	0.03
Maximum	14.4	1,886	1,529	0.06

Shown is the climatic profile for *E. regnans* calculated by Lindenmayer *et al.* (65). GEP is estimated from a regression correlation derived from flux tower data as a function of mean annual temperature by Law *et al.* (34). k is the decomposition rate constant of coarse woody debris calculated from an empirical relationship derived by Chambers *et al.* (42) using forest biome characteristic temperatures.

Land-Use Activity. The final reason for high biomass carbon densities in *E. regnans* forests is a prolonged absence of direct human land-use activity. The O'Shannassy Catchment has been closed to public access for >100 years to provide water for the city of Melbourne. It had an almost complete absence of Indigenous land use before European settlement. Natural disturbances have included wildfire, windstorms, and insect attacks. Logging has been excluded, including postwildfire salvage logging that removes large amounts of biomass in living and dead trees (thus preventing the development of multiple age cohorts) (21, 51, 52).

Some types of temperate moist forests that have had limited influence by human activities can be multiaged and do not necessarily consist exclusively of old trees, but often have a complex multiaged structure of multiple layers produced by regeneration from natural disturbances and individual tree gaps in the canopy (53). Net primary production in some types of multiaged old forests has been found to be 50–100% higher than that modeled for an even-aged stand (54). Both net primary production and net ecosystem production in many old forest stands have been found to be positive; they were lower than the carbon fluxes in young and mature stands, but not significantly different from them (55). Northern Hemisphere forests up to 800 years old have been found to still function as a carbon sink (11). Carbon stocks can continue to accumulate in multiaged and mixed species stands because stem respiration rates decrease with increasing tree size, and continual turnover of leaves, roots, and woody material contribute to stable components of soil organic matter (56). There is a growing body of evidence that forest ecosystems do not necessarily reach an equilibrium between assimilation and respiration, but can continue to accumulate carbon in living biomass, coarse woody debris, and soils, and therefore may act as net carbon sinks for long periods (12, 57–59). Hence, process-based models of forest growth and carbon cycling based on an assumption that stands are even-aged and carbon exchange reaches an equilibrium may underestimate productivity and carbon accumulation in some forest types.

Large carbon stocks can develop in a particular forest as a result of a combination and interaction of environmental conditions, life history attributes, morphological characteristics of tree species, disturbance regimes, and land-use history. Very large stocks of carbon occur in the multiaged and multilayered *E. regnans* forests of the Central Highlands of Victoria. The same suite of factors listed above operate, to varying degrees, across other evergreen temperate forests, particularly in the northwestern United States, southern South America, New Zealand, and elsewhere in southeastern Australia. Collectively, they provide the basis of a generalized framework for predicting high biomass carbon density forests. However, construction of a quantitative predictive model inclusive of all factors is complicated by a lack of process understanding (37), knowledge of species life history characteristics and dynamics, and many interactions and feedback effects (60).

Climate Change Policy Implications

Our results about the magnitude of carbon stocks in forests, particularly in old forests that have had minimal human disturbance, are relevant to negotiations under the United Nations Framework Convention on Climate Change (UNFCCC) concerning reducing emissions from deforestation and forest degradation. In particular, our findings can help inform discussions regarding the roles of conservation, sustainable management of forests and enhancement of forest carbon stocks (ref. 61; http://unfccc.int/resource/docs/2007/cop13/eng/06a01.pdf#page=8). Conserving forests with large stocks of biomass from deforestation and degradation avoids significant carbon emissions to the atmosphere, irrespective of the source country, and should be among allowable mitigation activities negotiated through the UNFCCC for the post-2012 commitment period. Similarly, where practical, management that allows restoration of a forest's carbon sequestration potential should be a recognized mitigation activity.

Our insights into forest types and forest conditions that result in high biomass carbon density can be used to help identify priority areas for conservation and restoration. The global synthesis of site data (Fig. 3 and Table 2) indicated that the high carbon densities of evergreen temperate forests in the northwestern United States, southern South America, New Zealand, and southeastern Australia should be recognized in forest biome classifications.

Concluding Comments

Our findings highlight the value of field-based site measurements in characterizing forest carbon stocks. They help reveal the variability within forest biomes and identify causal factors leading to high carbon densities. Further analyses of existing site data from forests around the world, along with new field surveys, are warranted to improve understanding of the spatial distribution of biomass carbon inclusive of land-use and fire history.

Methods

Biomass of *E. regnans* Forest. The 13,000-ha O'Shannassy Catchment (37.62° S, 145.79° E) has a mean annual rainfall of 1,670 mm, mean annual temperature of 9.4 °C, and annual radiation of 178 $W \cdot m^{-2}$. Average elevation of the catchment is 830 m, and the area has a generally southerly aspect. Soils are deep red earths overlying igneous felsic intrusive parent material. These are fertile soils with high soil water-holding capacity and nutrient availability compared with most forest soils in Australia. The vegetation is classified as tall eucalypt forest with small pockets of rainforest. The forest is multilayered with an overstory of *E. regnans*, a midstory tree layer of *Acacia dealbata*, *A. frigiscens*, *Nothofagus cunninghamii*, and *Pomaderis aspera*, and a tall shrub layer that includes the tree ferns *Cyathea australis* and *Dicksonia antarctica*.

Inventory sites were established by using a stratified random design to sample the range in dominant age cohorts across the catchment. Stands were aged by a combination of methods, including historical records of disturbance events, tree diameter–age relationships, and cross-checking with dendrochronology. Ages of understory plants ranged from to 100 to 370 years, as determined by radiocarbon dating (62). Different components of the ecosystem survive and regenerate from various previous disturbance events. All living and dead plants >2 m in height and >5 cm in diameter were measured at 318 10-m × 10-m plots nested within 53 sites (each measuring 3 ha) within the catchment. Tree size ranged from 486-cm diameter at breast height (DBH) to 84 m in height (Fig. 1).

Living and dead biomass carbon for each site were calculated by using an allometric equation applied to the inventory data for the individual trees in the plots. The equation related biomass to stem volume and wood density. A reduction factor was included in the equation to account for the reduction in stem volume caused by asymmetric buttresses, based on measurements of stem cross-sections and the area deficit between the actual wood and the perimeter derived from a diameter measurement (43). A second reduction factor was included in the equation to account for decay and hollows in stems of *E. regnans* calculated as a proportion related to tree size. Trees >50 cm DBH begin to show signs of internal decomposition, and by 120 cm DBH actual tree mass is ≈50% of that predicted from stem volume (52). Accounting for decay is an important aspect of estimating biomass from allometric equations derived from stem volume that requires further research, but that is overcome by using direct biomass measurements for the derivation of the allometric equations. Selection of trees for measurement that cover the full range of conditions is also important. Unlike many allometric equations developed for forest inventory purposes, the equation used here was calculated from data representing ecologically mature *E. regnans* trees. Carbon in dead biomass was calculated by using this allometric equation for standing stems with a reduction for decay. Coarse woody debris on the forest floor was measured along 100-m transects (63). The structure of stands with high biomass was described by a bimodal frequency distribution of tree sizes that represented different age cohorts. The maximum amount of biomass carbon occurred in tree sizes 40–100 and 200–240 cm DBH. A lack of comparable high-quality soil data meant we could not provide estimates of below-ground carbon stocks nor consider associated soil carbon dynamics.

Our analyses of biomass carbon stocks used a combination of techniques including field inventory data, biomass measurements, and understanding of carbon cycling processes, as has been recommended by the IPCC (64). The relationship between reflectance from spectral bands, leaf area index, and biomass accumulation is not linear. This is exemplified by the relatively low leaf area of *E. regnans* for the high biomass accumulation in the stemwood of these tall trees. Hence, it is important that all of these types of information are used to estimate biomass carbon stocks and that models are well calibrated with site data, rather than relying solely on remote sensing.

Global Site Biomass Data. Data on forest biomass were obtained from the literature where biomass was calculated from individual plot data at sites that represent largely mature or primary forest with minimal human disturbance (Table S1). The data were categorized into forest biomes (defined by the IPCC; Table 4.5 in ref. 4). We used field plot data that were available in the published literature as they constitute the most reliable primary data sources. We did not use modeled estimates of biomass carbon or regional estimates derived from forest inventory data and expansion factors to derive wood volume and biomass. A carbon concentration of 0.5 $gC \cdot g^{-1}$ was used where only biomass data were provided. Where site information was not given, latitude and longitude were obtained from Google Earth (http://earth.google.com) by using the described site location, and mean annual temperature and precipitation were obtained from a global dataset (www.cru.uea.ac.uk/cru/data/tmc.htm). Little or no information was provided by most of the publications concerning how internal decay in trees was accounted for in the biomass estimates. Hence, our estimates of biomass of *E. regnans* that were reduced to account for decay are considered conservative compared with the global site data.

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Supporting Information

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SI Text

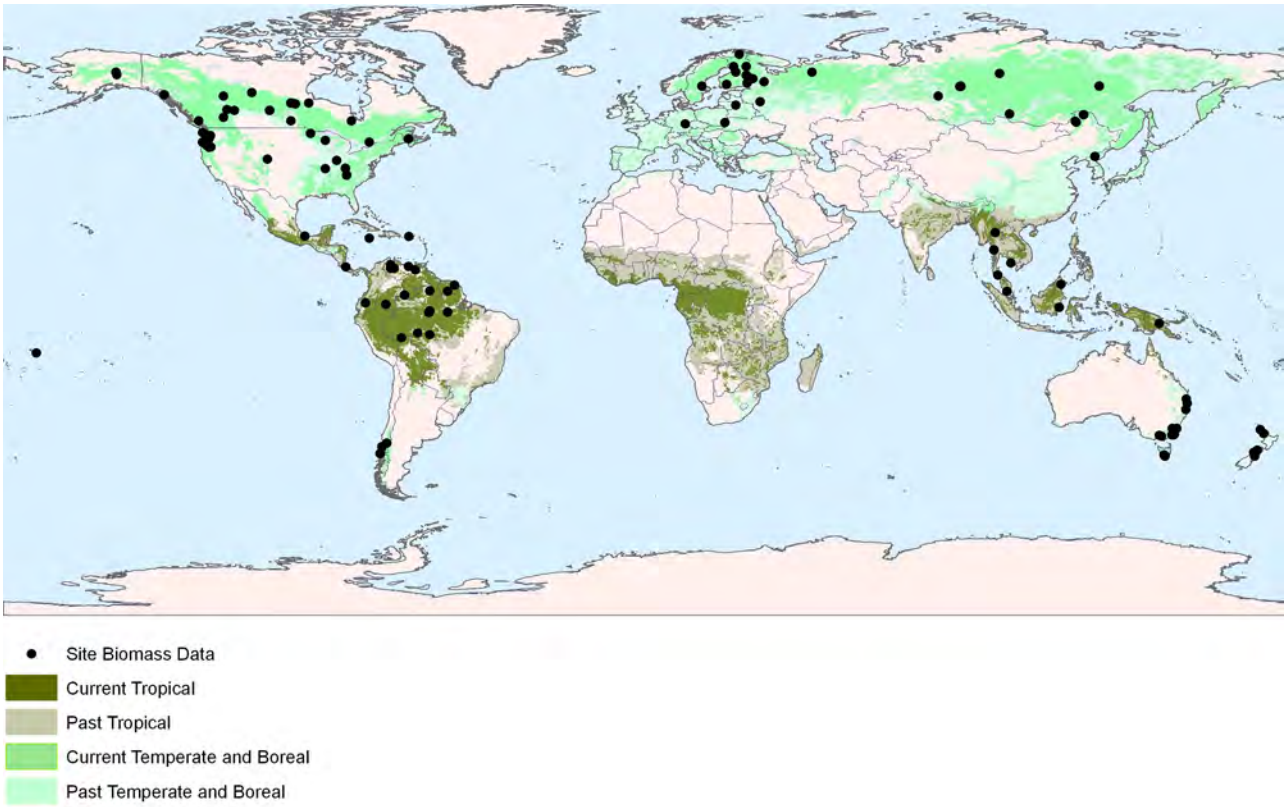

Fig. S1. Distribution of sites with data for biomass carbon from the published literature is shown in relation to global biomes of tropical, temperate, and boreal forest, with their current and original extent. The map of the global distribution of current and original forest areas was obtained from United Nations Environment Programme, World Conservation Monitoring Centre, Global Forest Cover Map.

Table S1. Global sites with biomass data used to analyze trends across forest biomass and to compare with *E. regnans* forests in Australia

Region	Site	Species	Latitude	Longitude	Mean annual temperature, °C	Mean annual precipitation, mm	Aboveground living biomass carbon, tC·ha^{-1}	Total living + dead biomass carbon, tC·ha^{-1}	Ref.
Tropical forest									
Tropical wet									
Central America	Los Tuxtlas, Mexico	tropical, tall evergreen	18.58°N	95.08°W	27.0	4700	181	195	1
	La Selva Biological Station, Costa Rica	tropical wet rainforest	9.85°N	83.60°W	26.0	4000	87		2
South America	Tapajos NF, Brazil	tropical rainforest	3.04°N	54.95°W	25.0	2000	141	202	3,4,5
	Northern Rôndonia State	tropical moist forest	8.75° S	63.38°W	26.2	2300	143	163	6
	Rondonia	upland tropical evergreen forest	9.20°S	60.05°W	25.2	2354	195		7
	Manaus, Central Amazon	tropical evergreen forest	2.50°S	60.00°W	26.7	2200	162		8
	Manaus, Central Amazon	tropical upland moist forest	2.97°S	60.18°W	26.7	2285	180		9
	Rio Negro, Venezuela	tropical moist forest	1.93°N	67.05°W	24.9	3500	117	159	10
	Venezuela	tropical moist forest	9.00°N	64.00°W	25.5	2850	179	227	11
	San Carlos, Venezuela	evergreen sclerophyllous woodland	1.92°N	67.07°W	26.0	3600	182	320	12
	San Carlos, Venezuela	tropical evergreen lowland forest	1.92°N	67.07°W	26.0	3600	138	350	13
	Araracuara, Colombia	ombtophilous tropical rainforest	0.63°S	72.37°W	25.5	2998	175		14
	French Guiana	tropical wet rainforest	4.75°N	53.00°W	25.8	2757	155		15
Oceania	Tutuila Island, Samoa	lowland tropical rainforest	14.30°S	170.68°W	26.9	3207	122		16
Asia	Khao Chong, peninsular Thailand	tropical rainforest	7.50°N	99.80°E	27.2	2700	182		17
	Cheko, Cambodia	evergreen seasonal forest	10.93°N	103.40°E	27.8	3726	191		18
	Ulu Segama FR, Sabah, Malysia	dipterocarp hill forest	5.00°N	117.50°E	26.7	2700	165		19
	Marafunga, New Guinea	lower montane rainforest	6.00°S	145.18°E	13.0	4000	387		20
Tropical moist									
Central America	Eastern Jamaica	montane rainforest	18.00°N	77.00°W	24.4	1685	204	204	21
	Luquillo, Puerto Rico	*Prestoea montana,* tropical palm forest	18.42°N	65.92°W	19.7	1885	224	298	22
South America	Manaus, Central Amazon, Brazil	tropical rainforest	3.10°N	60.03°W	27.4	1571	237	399	23
	Tapajos, Central Amazon	tropical forest	2.85°S	54.97°W	25.0	1920	153	161	24
	Tapajos, Central Amazon	tropical upland moist forest	2.85°S	54.97°W	24.5	1909	141		9
	Rio Branco, western Amazon	open forest	10.12°S	68.00°W	25.0	1940	95		9
	Venezuela	tropical transition moist to dry forest	9.50°N	70.00°W	26.0	1500	148	178	11
Asia	Sebulu, East Kalimantan, Indonesia	tropical lowland evergreen dipterocarp rainforest	1.50°S	116.97°E	27.0	1862	254		25
	Sebulu, East Kalimantan, Indonesia	tropical lowland evergreen dipterocarp rainforest	1.50°S	116.97°E	27.0	1862	436		26
	Pasoh FR, Negeri Sembilan, Malaysia	lowland tropical rainforest	2.97°N	102.30°E	28.0	1842	215		27,28
	Thong Pha Phum NF, Thailand	tropical rainforest	14.67°N	98.68°E	25.0	1650	138		29
	Thong Pha Phum NF, Thailand	dry evergreen forest	14.67°N	98.68°E	25.0	1650	70		29
	Thong Pha Phum NF, Thailand	mixed deciduaous forest	14.67°N	98.68°E	25.0	1650	48		29
	Ping Kong, northwestern Thailand	monsoon forest	19.50°N	99.00°E	24.0	1364	146		17
Tropical dry									
South America	Venezuela	tropical dry forest	10.00°N	66.00°W	27.0	800	70	111	11
Tropical montane									
South America	Venezuela	tropical lower montane moist forest	9.50°N	71.00°W	15.0	1487	173	235	11
	Venezuela	tropical montane wet forest	10.50°N	71.00°W	10.5	1968	157	211	11
	Eastern Andean Mts., Ecuador	*Polylepis incana,* high altitude	0.22°S	78.05°W	7.2	1500	163		30
Temperate forest									
Warm temperate moist									
North America	Alaskan coast	*Tsuga heterophylla, Chamaecyparis nootkatensis, T. mertensiana*	58.37°N	134.72°W	10.0	3550	325	582	31
	Oregon Cascades	*Pseudotsuga menziesii*	44.00°N	122.50°W	10.1	1789	331	526	32
	Oregon coast	*Tsuga heterophylla-Picea sitchensis*	45.00°N	123.93°W	10.1	3115	436	626	32

Region	Site	Species	Latitude	Longitude	Mean annual temperature, °C	Mean annual precipitation, mm	Aboveground living biomass carbon, tC·ha^{-1}	Total living + dead biomass carbon, tC·ha^{-1}	Ref.
	Oregon	*Abies amabilis; Pseudotsuga menziesii*	44.00°N	122.67°W	10.1	1789	440	514	32
	Washington	*Abies amabilis; Pseudotsuga menziesii*	47.00°N	122.67°W	10.1	1789	422	496	32
	Washington	*Pseudotsuga menziesii*	46.00°N	122.00°W	12.5	1000	278	473	33
	Great Smoky Mt.	deciduous mesic	35.67°N	83.38°W	10.3	1744	199		34
	Southern Appalachians	Cove forests	35.68°N	83.42°W	12.7	1306	236		35
	Indiana	*Quercus shumardii, Liquidamber styraciflua*	39.83°N	86.18°W	11.0	1028	117		36
	Kentucky	*Fagus grandifolia, Quercus alba*	37.72°N	83.80°W	12.7	1230	165		37
	Illinois	*Carya ovata, Quercus velutina*	37.52°N	89.32°W	14.4	1270	131		38
South America	Chile	*Nothofagus dombeyi, Drimys winteri, N. nitida, Aextoxicon punctatum*	40.50°S	73.50°W	10.6	1600	142		39
Australasia	Auckland & Northland, NZ	*Agathis australis*	35.72°S	173.63°E	13.9	1640	672	982	40
	Auckland & Northland, NZ	*Agathis australis*	36.90°S	174.57°E	14.4	1341	312	400	40
	Maimai, South Island NZ	*Nothofagus truncata, Podocarpus ferrugineus*	42.16°S	171.75°E	10.9	2600	153	352	41
	Nelson, South Island NZ	*Nothofagus truncata*	41.52°S	172.75°E	10.5	1307	166	289	42
	NSW south coast, Aust.	*E. fastigata, E. sieberi, Corymbia maculata*	35.47°S	150.11°E	13.8	1097	447	615	43
	Gippsland, Aust	*E. fastigata, E. obliqua, E. cypellocarpa*	37.28°S	149.15°E	10.4	1165	310	489	P. Gibbons
	NSW south coast, Aust.	*E. fastigata, E. sieberi, Corymbia maculata*	35.60°S	149.88°E	10.8	1090	270	487	B. Mackey
	northern NSW, Aust.	*Caldluvia paniculosa, Geissois benthami*	28.50°S	153.00°E	18.9	1192	182	252	44
	NSW south coast, Aust.	*E. sieberi, E. agglomerata, E. obliqua*	37.00°S	149.50°E	11.2	1051	218	319	45
	montane, south east Aust.	*E. delegatensis*	35.37°S	148.83°E	10.3	1185	199	333	H. Keith
	southern NSW & Vict., Aust.	*E. bridgesiana, E. cypellocarpa, E. muellerana*	37.26°S	148.71°E	11.2	1041	294	433	A. Claridge
	southern Qld., Aust.	*Argyrodendron*	27.33°S	152.75°E	17.0	1448	224	310	46
	central Victoria, Aust.	*E. regnans*	37.43°S	145.18°E	10.4	1244	678	1000	47
	northern NSW, Aust.	*E. pilularis*	30.33°S	152.64°E	15.2	1467	298	477	48
Cool temperate moist									
North America	Oregon coast	*Tsuga heterophylla-Picea sitchensis*	45.00°N	123.90°W	8.6	2575	465	762	49
	Washington coast	*Tsuga heterophylla-Picea sitchensis*	47.70°N	123.90°W	8.5	3356	364	624	49
	Oregon Cascades	*Pseudotsuga menziesii* dominated	44.20°N	122.20°W	8.4	2002	432	707	49
	Washington Cascades	*Abies amabilis; Tsuga heterophylla*	46.80°N	121.70°W	6.4	2375	380	636	49
	Oregon Cascades	*Pseudotsuga menziesii*	44.00°N	122.50°W	8.5	2300	356	568	50
	Oregon Cascades	*Pseudotsuga menziesii*	44.00°N	122.50°W	8.5	2300	587	794	51
	Washington Cascades	*Abies amabilis*	46.80°N	121.70°W	5.4	2700	224	781	52
	Colorado, Rocky Mt. NP	*Picea engelmannii, Abies lasiocarpa*	40.28°N	105.63°W	1.5	1000	124	289	53
South America	Cordillera de Piuchue, Chile	*Nothofagus dombeyi, Drimys winteri, Laureliopsis philippiana*	42.50°S	74.00°W	7.2	5000	179	395	54,55,56
	Cordillera de Piuchue, Chile	*Fitzroya cupressoides*	42.50°S	74.00°W	7.2	5000	268	450	54,55,56
	Cordillera de Piuchue, Chile	*Philgerodendron uviferum, Tepualia stipularis*	42.50°S	74.00°W	7.2	5000	146	326	54,55,56
	San Pablo de Tregua, Andes, Chile	*Nothofagus dombeyi, Laureliopsis philippiana, Saxegothaea conspicua*	39.63°S	72.08°W	9.7	2400	439	571	57
	San Pablo de Tregua, Andes, Chile	*Laureliopsis philippiana, Saxegothaea conspicua, Dassyphyllum diacanthoides*	39.63°S	72.08°W	9.7	2400	332	428	57
Australasia	Central South Island NZ	*Nothofagus solandri*	43.25°S	172.00°E	8.0	1447	123	150	58
	Central Highlands, Vict., Aust.	*Eucalyptus regnans*	37.62°S	145.79°E	9.4	1668	501	1141	D. Lindenmayer
	southern Tasmania, Aust.	*E. obliqua*	43.21°S	146.70°E	9.8	1722	444	673	H. Keith

Region	Site	Species	Latitude	Longitude	Mean annual temperature, °C	Mean annual precipitation, mm	Aboveground living biomass carbon, tC·ha^{-1}	Total living + dead biomass carbon, tC·ha^{-1}	Ref.
	southern Tasmania, Aust.	*E. regnans*	42.83°S	146.57°E	8.6	1503	752	1302	59
	southern Tasmania, Aust.	*E. obliqua*	43.09°S	146.70°E	9.9	1490	668	956	59
Cool temperate dry									
North America	Eastern Oregon	*Pinus ponderosa-Pinus contorta*	43.70°N	121.60°W	6.2	497	85	157	49
	Wisconsin	*Tsuga canadensis: Pinus strobus*	45.50°N	89.33°W	5.3	800	286	476	60
	Oregon, Waldo Lake	*Tsuga mertensiana, Pinus contorta, Pinus monticola*	43.50°N	122.00°W	4.6	404	158	202	61
Cool temperate montane									
Asia	Changbai, China	*Acer mono, Betula costata,Pinus koraiensis, Tilia amurensis*	41.00°N	127.00°E	3.9	782	147	153	62
Boreal forest									
Boreal moist									
North America	Minnesota, USA	*Picea marina*	47.50°N	93.50°W	4.1	690	34		63
	Alberta, Canada	*Pinus contorta, Populus tremulous, Picea glauca*	54.25°N	117.00°W	2.6	500	50	79	64
	Thompson, Manitoba, Canada	*Picea marina* - dry	55.80°N	97.87°W	0.1	536	72	116	65
	Thompson, Manitoba, Canada	*Picea marina* - wet	55.80°N	97.87°W	0.1	536	31	53	65
	Manitoba, Canada, BOREAS NSA	*Picea marina*	55.99°N	98.99°W	-4.6	536	57	74	66,67
	Manitoba, Canada, BOREAS NSA	*Pinus banksiana*	55.99°N	98.99°W	-4.6	536	29	50	66,67
	Manitoba, Canada, BOREAS NSA	*Populus tremuloides*	55.99°N	98.99°W	-4.6	536	57	92	66,67
	Canada - Atlantic Maritime		46 °N	66 °W	5.0	1200	87		68
	Canada - Mixedwood Plains		45 °N	77 °W	6.5	860	113		68
	Canada - Pacific Maritime		51 °N	125 °W	6.7	2250	80		68
	Canada - Montane Cordillera		52 °N	118 °W	4.0	1000	107		68
	Canada - Hudson Plains		56 °N	94 °W	-3.0	600	34		68
	Canada - Eastern Boreal Shield		51 °N	82 °W	5.5	1000	67		68
Siberia	Zotino	*Pinus sylvestris*	60.73°N	89.15°E	-3.3	663	75	92	69
	Karelia, Russia	*Picea abies*	62.00°N	34.00°E	2.2	650	38		70
	Tomsk, Russia	*Pinus sylvestris*	58.00°N	83.00°E	-0.8	501	81		71
Europe	Fyedorovskoye, European Russia	*Picea abies*	56.45°N	32.92°E	3.6	714	95		69
	Waldstein, Germany	*Picea abies*	50.15°N	11.87°E	5.8	1100	105		69
	Tampere, southern Finland	*Pinus sylvestris, Picea abies, Betula pendula, B. pubescens*	61.28°N	23.44°E	4.0	548	102	153	72
	Rovaniemi, northern Finland	*Pinus sylvestris, Picea abies, Betula pendula, B. pubescens*	66.34°N	25.50°E	0.5	591	77	116	72
	Kangasvaara, eastern Finland	*Picea abies, Pinus sylvestis, Betula pubescens, Populus tremula*	63.85°N	28.97°E	1.2	709	82	123	73
	Central Finland	*Pinus sylvestris*	64.72°N	26.02°E	2.0	500	34	67	74
	Southern Finland	*Pinus sylvestris*	61.65°N	29.28°E	4.0	550	28	64	74
	Lithuania	*Pinus sylvestris*	55.42°N	26.02°E	6.0	760	75	133	74
	southern Poland	*Pinus sylvestris*	50.47°N	22.98°E	8.0	600	68	143	74
	Llomantsi, Finland	*Picea abies, Pinus sylvestis, Betula pubescens*	62.85°N	30.88°E	1.7	640	25		75
	Jädraås, Sweden	*Pinus sylvestris*	60.82°N	16.50°E	3.0	731	29		76,77
	Oulu, Finland	*Picea excels*	66.37°N	29.00°E	0.0	500	51		78
Boreal dry									
North America	Alaska, USA	*Picea glauca, P. marina, Populus/Alnus, Betula papyrifera*	64.75°N	148.25°W	-3.5	269	61		79
	Alaska, USA	*Picea marina*	64.00°N	148.00°W	-3.4	275	43		80
	Saskatchewan, Canada, BOREAS-SSA	*Picea marina*	53.99°N	104.99°W	-1.1	405	49	66	66,67
	Saskatchewan, Canada, BOREAS SSA	*Pinus banksiana*	53.99°N	104.99°W	-1.1	405	35	63	66,67

Region	Site	Species	Latitude	Longitude	Mean annual temperature, °C	Mean annual precipitation, mm	Aboveground living biomass carbon, tC·ha^{-1}	Total living + dead biomass carbon, tC·ha^{-1}	Ref.
	Saskatchewan, Canada, BOREAS SSA	*Populus tremuloides*	53.99°N	104.99°W	-1.1	405	93	136	66,67
	Canada - Taiga Plains		58 °N	118 °W	-5.5	350	99		68
	Canada - Western Taiga Shield		59 °N	110 °W	-4.0	350	47		68
	Canada - Western Boreal Shield		51 °N	99 °W	-4.0	400	33		68
	Canada - Boreal Plains		54 °N	115 °W	0.0	462	113		68
Siberia	Yakutsk	*Larix gmellinii*	60.85°N	128.27°E	-10.0	213	55		69
	Central Siberia	*Pinus sylvestris, lichen*	60.75°N	89.41°E	-3.7	493	62		81
	Central Siberia	*Pinus sylvestris, Vaccinium* mosses	60.73°N	89.32°E	-3.7	493	149		81
	Central Siberia, Yenisei River	*Pinus sylvestris, lichen*	60.72°N	89.13°E	-3.7	493	65	88	82
	Central Siberia, Yenisei River	*Pinus sylvestris, Vaccinium* mosses	60.72°N	89.13°E	-3.7	493	121	152	82
	Koinas, Russia	*Picea abies*	64.67°N	47.50°E	-1.2	499	66		80
	Irkutsk	*Pinus sylvestris*	53.00°N	103.00°E	-1.2	470	71		83
	Yakutsk	*Larix gmelinii*	60.85°N	128.27°E	-9.6	213	18		83
	Tura	*Larix gmelinii*	64.32°N	100.22°E	-9.5	322	11		84
Europe	northern Finland	*Pinus sylvestris*	69.73°N	27.02°E	-1.0	450	14	54	74
Asia	China, Daxing'anling	*Larix gmelinii*	50.83°N	121.50°E	-5.4	500	26		85
	China, Daxing'anling	*Larix gmelinii*	50.68°N	121.84°E	-4.0	425	31		86
	China, Daxing'anling	*Larix gmelinii-Ledum*	52.73°N	123.83°E	-3.0	425	28	54	87
	China, Daxing'anling	*Larix gmelinii-grass*	52.73°N	123.83°E	-3.0	425	30	40	87
	China, Daxing'anling	*Larix gmelinii-Rhododendron*	52.73°N	123.83°E	-3.0	425	93	101	87

Canadian sites from ref. 59 are average values from plots within a region, where the individual plot data were not provided in the reference.

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Sediment Production in a Coastal Watershed: Legacy, Land Use, Recovery, and Rehabilitation[1]

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Abstract

Sediment production has been measured for nearly half a century at the Caspar Creek Experimental Watersheds. Examination of this sediment record provides insights into the relative magnitudes and durations of sediment production from management practices including road construction, selection harvest and tractor skidding, and later road-decommissioning. The 424-ha South Fork was harvested under standards that applied before passage of the 1973 Forest Practice Act. Regression analysis of annual suspended sediment loads on peak flows indicates that sediment production roughly doubled, with a return to pre-treatment levels about 11 years after harvest ended. However, sediment production again increased in the 1990s as road crossings deteriorated in response to large storms. Road crossings decommissioned in 1998 eroded a volume equivalent to more than half of the total yield in 1999 and enlarged another 20 percent over the last decade. Suspended sediment yields since decommissioning were reduced only for small storms. Recent assessment of 1970's era roads and skid trails found 443 remaining stream and swale crossings. Stream crossing have eroded an average volume of 10 m^3. Stream diversions are common, and many sites have the potential for future diversion. Diversions along incised roads and skid trails contribute to episodic sediment inputs. Mainstem sediment loads are elevated relative to those at tributary gages located above the decommissioned riparian haul road, indicating that sediment yields at the weir are enhanced along the mainstem itself. Since turbidity monitoring began in 1996, South Fork mainstem turbidities have exceeded ecosystem thresholds of concern a higher percentage of time than those in the North Fork.

Key words: erosion, legacy, logging, sediment, roads, road decommissioning

Introduction and site description

Two centuries of logging in the redwood forests of northern California have transformed the region. Although the redwoods remain the defining natural characteristic of this "other California", the landscape has been altered in a myriad of ways, some obvious and some subtle. Management activities such as timber harvest, road construction and use, and site preparation have been shown to deliver sediment, nutrients, and other pollutants to streams. Temporal and spatial variability of management impacts continues to be a topic of major concern—one that long-term research is particularly suited to address (Anderson and Lockaby 2011). The Caspar Creek Experimental Watersheds are a source of such data for the region.

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The Caspar Creek research watersheds are within the Jackson Demonstration State Forest, 5 km from the Mendocino coast. Streamflow and sediment data are collected from weirs constructed in 1962 on the 424 ha South Fork and 473 ha North Fork and from tributary gages installed between 1983 and 2001 (*fig. 1*). Over a 20-year period of rapidly evolving management practices, the 100-year-old 2nd-growth redwood and Douglas-fir forest of this coastal basin was selectively tractor-logged (South Fork, 1971 to 1973) and partially cable clear-cut (North Fork, 1985 to 1992). New roads were constructed in both watersheds in conjunction with timber harvest. A 4.7 km mainline riparian road was built in South Fork 4 years prior to harvest and decommissioned in 1998, 25 years post-harvest. These varied treatments influence hydrologic processes, recovery time-frames, and restoration responses.

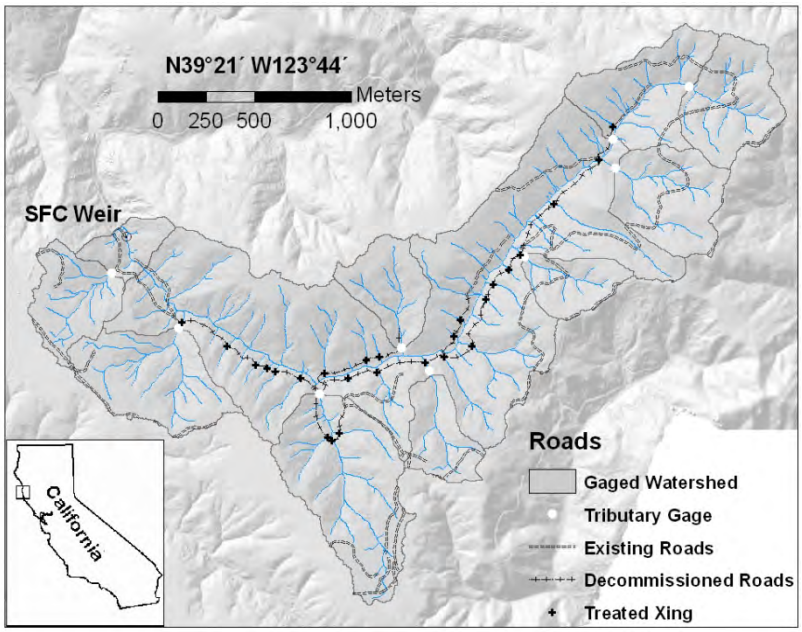

Figure 1—South Fork Caspar Creek watershed.

Several reports document enhanced sediment production in response to South Fork road construction, logging, and tractor-yarding (Lewis 1998, Rice et al. 1979, Tilley and Rice 1977). These prior reports rely on North Fork comparisons for estimates of South Fork sediment increases. Lewis (1998) found suspended sediment in the South Fork increased 335 percent the year after road construction, while yields for the next 3 years did not increase significantly. For the 6 years following logging, suspended sediment yields increased an average of 212 percent over expected values, or 331 percent when North Fork yields were adjusted to remove the effect of a large 1974 North Fork landslide. Suspended sediment yields recovered to background levels by 1979 and remained at background levels until 1985, when logging in the North Fork began. This report re-examines South Fork (SFC) suspended sediment trends through 2010 using analyses independent of North Fork (NFC) data and addresses the analytical problems presented by changing sampling protocols and episodic perturbations resulting from large landslides. Results are reviewed in light of erosion trends documented during 4 decades of field studies.

Methods

Sediment production estimates in the two watersheds are derived from water samples collected at the weirs (suspended loads) and annual bathymetric surveys of weir pond deposition. Pond deposition consists of approximately 40 percent suspended sediments and 60 percent bedload (Lewis 1998). Suspended sediment sampling protocols evolved over time. Initially, rising-limb data from fixed-stage siphon samplers were supplemented with manual DH-48 sampling during receding flows. Pumping samplers have been the primary means of suspended sediment sampling since 1976. Sediment concentrations, derived using standard gravimetric methods, were used to estimate loads using flow-duration sediment rating curves. Instream turbidimeters, deployed in 1996, are currently used in conjunction with pumped and DH-75 water samples to refine load estimates according to Turbidity Threshold Sampling protocols (Lewis and Eads 2009). Storm events are defined as the hydrograph rise to, and the ensuing recession from, a peak discharge exceeding 1.6 L/s per ha (0.17 yr recurrence interval).

Annual loads include an estimate of sediment flux between storm events and have been multiplied by a factor of 0.45 for years 1963 to 1975 to remove bias introduced by fixed-stage samplers. Lewis (1998) demonstrated the bias introduced by disproportionate sampling of rising hydrographs and the strong correlation between annual suspended loads and annual runoff. Using NFC calibration data, Lewis (personal communication, 2007) regressed annual loads on annual peaks and compared deviations to conclude that estimates prior to the 1976 change in sampling protocol are consistently higher than those of the subsequent period by a factor of 2.22 and proposed this same correction for both NFC and SFC annual loads.

To allow SFC sediment loads to be analyzed after 1985, when logging began in the North Fork control watershed, the present study employs a calibration relation between SFC annual suspended sediment loads and SFC annual maximum peakflows, using 1963 to 1967 and 1984 to 1992 data. The calibration relation is used to estimate expected annual loads under pretreatment (and post-recovery) conditions, and observed loads can then be compared with expected loads to calculate deviations associated with road construction, harvest, and later road decommissioning. A similar approach was taken using storm-based loads and peaks for the 1986 to 2009 data set to explore changes associated with road decommissioning.

The potential implications of altered sediment loads are evaluated using the 15 years of 10-min-interval turbidity now available for NFC and SFC. The number of days per year with turbidities exceeding the stream ecosystem stress thresholds proposed for Northern California watersheds (Klein and others 2008) were compared between sites using a paired t-test.

Erosion features larger than 7.6 m^3 were mapped in 1994, and subsequently after peak flows exceeding the 4 year return period (1997, 1998, and 1999). Beginning in 2000, this inventory was repeated on an annual basis. Slide dimensions and volumes were recorded.

Between 2004 and 2006, an inventory of legacy sediment sources was performed in the South Fork watershed based on protocols used for the Sinkyone Wilderness State Park Road Rehabilitation Project (Merrill 2003). Untreated roads and skid trails were evaluated in the field, using 2-m LiDAR and 1975 air photo imagery to help

locate the features. Stream and swale crossings, roads, landings, gullies, stream diversions (existing and potential), and landslide locations were mapped. In addition, the field crew attempted to remeasure voids from historic slides. At stream and swale crossings, erosion voids were measured to an accuracy of 20 percent, and erosion potential, the amount expected to erode over the next 3 decades, was estimated based on drainage area, vegetation, and bank condition.

Erosion measurements along the haul road decommissioned in 1998 (Keppeler and others 2007) were repeated in 2011. The field crew evaluated 35 treatment sites for "sediment delivery potential" and gully "activity level" (Merrill 2003). At 10 sites, thalweg profiles and three to five cross-section transects were surveyed using control points established in 1999 to estimate erosion in the intervening period.

Results

Regression results confirmed the strong correlation between annual suspended sediment load and peakflow (r^2 = 0.90), allowing prediction of SFC loads independently of NFC measurements. SFC suspended sediment loads averaged 44 t/km^2 per year during the 1962 to 1967 calibration period while NFC averaged 56 t/km^2 per year (68 ± 40 (0.95 CI) for 22 pre-treatment years). This revised analysis, correcting for sampler bias, resulted in an estimate of excess suspended sediment produced post-logging of 928 t/km^2 (116 t/km^2 per year) through 1979 (*fig. 2*).

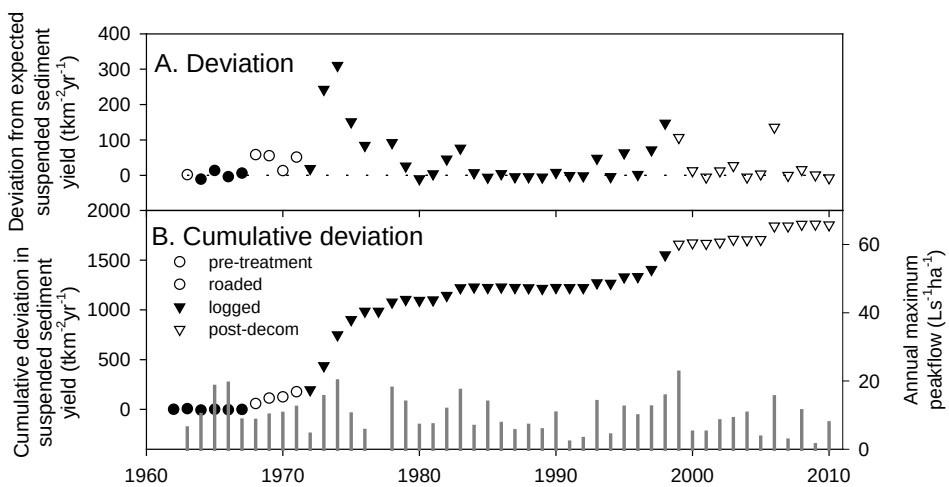

Figure 2—Excess suspended sediment production by year for (A) annual and (B) cumulative deviation from predicted load.

Beginning about 10 years after timber harvest, sediment production returned to pre-harvest levels, and this pattern persisted for another decade. Elevated sediment production was renewed in 1993 and was most evident during years with peak flows larger than the 4 year return interval flow (about 12 L/s per ha). Keppeler and Lewis (2007) detected SFC storm load increases of about 40 percent during 1998 to 2003, suggesting an episode of elevated sedimentation spanning the decommissioning treatment. Regression analyses of SFC storm loads on storm peaks for 1986 to 1998 and 2000 to 2009 show no significant difference ($p < 0.05$) after decommissioning for peaks larger than the 0.4 yr recurrence interval, but for smaller peaks, loads were significantly reduced (*fig. 3*).

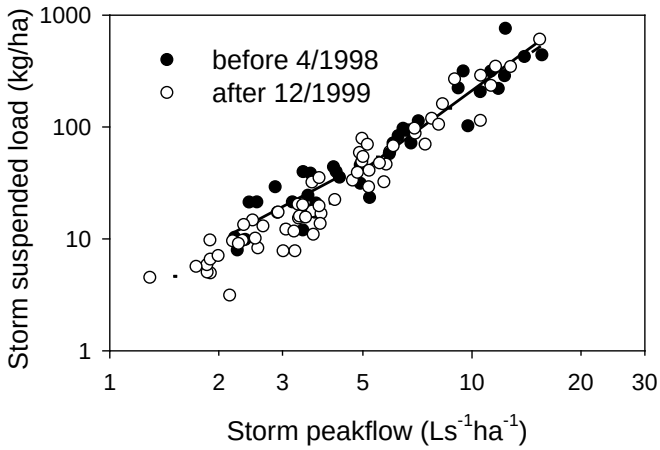

Figure 3—Sediment loads as a function of storm peak before and after decommissioning, divided into two peak discharge classes at the 0.4 yr return period.

Since implementation of continuous turbidity monitoring in 1996, SFC turbidities have exceeded ecosystem thresholds of concern more commonly than NFC turbidities. When turbidity records were tallied by stream ecosystem stress thresholds exceeding 25 (moderate), 50 (severe), 100 ntu (extreme) (Klein and others 2008) for each hydrologic year, SFC averages exceeded NFC's by 50, 60, and 120 percent ($p < 0.014$), respectively—a fairly consistent pattern even during years when NFC logging effects were evident. This result may reflect high inputs of fine sediments from road surfaces and bare ground in the South Fork, or may indicate that the physical properties of the sediment transported through the two weir ponds differ. The difference in ratios of average storm load above and below the two weirs supports the latter hypothesis. The weirs trap an estimated 20 to 30 percent of suspended sediment and virtually all bedload, thus the rationale for siting sampling stations ARF and QUE immediately upstream of the NFC and SFC weir ponds. Based on storm load data from 2001 to 2009, NFC transported just 70 percent of the load entering the pond, while SFC transported 80 percent.

Information from field-based sediment source assessments provides a context for interpreting the patterns of suspended sediment yield (*table 1*). The inventory of the entire South Fork watershed performed between 2004 and 2006 documented 443 remaining stream and swale crossings on untreated roads and skid trails. Of these, 325 had experienced partial failure. Swale crossings numbered 208, including 102 that had remained stable in the 3 decades since construction and only four that had eroded more than 10 m^3. In contrast, only 16 of 235 stream crossing had experienced no notable erosion. Eroded volume per stream crossing averaged 10 m^3, but most of this erosion did not appear to be recent. Fill material at risk of further erosion accounted for 16 percent of the estimated initial crossing fill. Stream crossings accounted for 82 percent of the "at risk" projection of erosion potential. Diversions onto roads and skid trails were common. Roughly 10 percent of stream crossings were active diversions while a similar number were "at risk" because a minor blockage could redirect flow onto the road surface. More than 300 m of entrenched diversions and active gullies were noted.

Table 1—*Field-based sediment source measurements (in-channel erosion from Reid and others 2010).*

Type	Years	m^3	m^3/yr	Method
Logging period				
landslides (re-assessed)	1971-76	7944	1324	inventory 2004-2006
Recovery period				
untreated crossing erosion	1971-06	2827	79	inventory 2004-2006
gully erosion	1971-06	932	26	inventory 2004-2006
mass-wasting > 7.6 m^3	1977-94	1705	95	inventory 1994
mass-wasting > 7.6 m^3	1977-06	2897	97	inventory 2004-2006
mass-wasting > 7.6 m^3	1995-99	4008	802	inventory, irregular
Post-decommission period				
mass-wasting > 7.6 m^3	2001-10	553	55	annual inventory
treated crossing erosion	1999	651	651	survey, 1999
treated crossing erosion	2000-01	108	54	survey, 2001-2002
treated crossing erosion	2002-11	150	15	survey, 2011
in-channel erosion	2001-08	na	291	survey, irregular

Landslide voids encountered during the recent inventory included 7944 m^3 (18.7 m^3/ha) from slides listed in the 1976 data set and 2897 m^3 (6.8 m^3/ha) in more recent features. However, half the slides in the 1976 data set were not relocated.

Soil displacement by mass-wasting for events larger than 7.6 m^3 declined since the 1970s and again in the most recent decade relative to the 1990s. Through 1994, the rate was 95 m^3/yr; from 1995 to 1999, 802 m^3/yr; and since 2000, 55 m^3/yr. Seven of 10 slides in the 1994 inventory were along haul roads and landings, but these accounted for less than 20 percent of the total volume. Only two failures along the mainline road were attributed to 1993. Between 1993 and 1999, 17 slides accounting for 70 percent of the mass-wasting volume occurred along the mainline road—15 resulted from culvert or fill failures. In the post-decommissioning data set, the largest feature was a 255 m^3 slide that originated along an untreated mid-slope road routing entrenched flow from a stream diversion to the fill slope. The slide traveled down the tributary channel as a debris torrent, depositing debris in the 1998 restored stream crossing void and continuing on to the South Fork mainstem.

Keppeler et al. (2007) report that the 1998 road decommissioning, followed by the largest peakflow of the 49 year SFC record, profoundly impacted sediment production in 1999. Re-evaluation of 35 treated crossings in 2011 indicated that erosion is ongoing at 31. Sediment transport potential was rated “high” or “extreme” at 12 of 37 sites. The predominant “Activity Class” (Merrill 2003) for the gullied crossings was “3” (indicating “good vegetative cover” with less than 50 percent of the incised area subject to erosion and transport). However, five were characterized as “1” (exhibiting “widespread transport and little or no vegetation”) and five were rated as “4” (supporting “good vegetative cover” and having gentle side-slopes).

The 2011 re-survey of channel cross-sections and profiles established at 10 sites in 1999 quantified additional scour and fill since 2001. Incision and widening were evident at 60 and 40 percent, respectively, of 42 cross-section transects, while 30 percent of transects showed neither. Mean profile elevation decreased by 0.09 m.

Headcut retreat was evident along all 10 surveyed profiles. In sum, these 10 sites enlarged by 80 m^3, or about 20 percent, since last assessed. Assuming a similar rate of erosion from the 25 sites that were not re-surveyed, total enlargement is estimated to have been about 150 m^3 over the last decade. A foot trail along the former road surface receives semi-regular (unsanctioned) bicycle and motorcycle use. The road has not fully revegetated and delivers an unknown amount of sediment to the stream.

Discussion

To relate erosion measurements to recent trends in suspended sediment yields at the weirs, it is helpful to compare unit-area sediment loads measured immediately upstream of the weirs with those measured at upstream tributary gages to identify areas contributing disproportionate amounts of sediment. Since 2000, when nine tributary gages were installed in the South Fork watershed, NFC event-based storm loads averaged 104.3 kg/ha based on contributions from the two gages delivering directly to the weir pond. Upstream gages produced similar loads, averaging 99.3 kg/ha. In contrast, South Fork event-based loads (the sum of mainstem loads measured 50 m upstream of the weir pond and the tributary gage load delivered directly to the weir pond) averaged 75.8 kg/ha. South Fork tributaries draining 52 percent of the watershed area produced 54.1 kg/ha per event, on average. Assuming the few small ungaged tributaries are not generating disproportionately high amounts of sediment, the SFC load is enriched below tributary gages and along the mainstem. Three of the tributary gages are sited within 42 m upstream of stream crossings restored during the 1998 decommissioning of the mainline road, and paired water samples were collected above and below the crossings during water years 2004 and 2006. These samples indicate suspended sediment concentrations were enriched below the decommissioned crossings ($p < 0.012$), reflecting the net contributions of erosion within the restored stream crossings and from the old road surface.

During the last decade, the volume of fine sediments in pools declined along the lower 490 m of mainstem channel above the SFC weir. However, pool depths decreased as well. Mainstem cross-sections, measured biennially since 2000 along 3100 m of channel, scoured 59 m^3 from 2000 to 2010[3]. It is likely that sediment inputs from both recent and historic mass-wasting, including materials eroded from failed and decommissioned crossings, were re-mobilized during high flows and augmented suspended sediment loads generated in upland portions of the South Fork watershed. In-channel erosion processes were also active in South Fork tributaries and account for a substantial portion of the suspended load at SFC (Reid et al. 2010).

Conclusions

Measured rates of suspended sediment yield in the South Fork Caspar Creek watershed were highest during the first decade after selection harvest and tractor-yarding was completed in 1973. A second episode of increased suspended sediment yield, coinciding with a notable increase in road-related mass-wasting, commenced 20 years post-harvest. Since decommissioning of the riparian road in 1998, reduced sediment yields have been detected only for small storms, though the incidence and

[3] S. Hilton, Hydrologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 2011, personal communication.

magnitude of mass-wasting was lower during the last decade than in the 1990s. Mainstem channel measurements and tributary gage data suggest that sediment deposited prior to 2000 was mobilized and transported during the last decade. Erosion in upland areas, including diversion-induced mass-wasting, incision of crossings along untreated roads and skid trails, and in-channel gullying, remains active. Potential interactions with persisting legacy effects should be considered when modern forest management practices are superimposed on landscapes still responding to past disturbances.

Acknowledgments

This study is part of the cooperative Caspar Creek research program instituted in 1960 by the U.S. Department of Agriculture, Forest Service Pacific Southwest Research Station and the California Department of Forestry and Fire Protection. Leslie Reid and Jack Lewis provided critical components of this analysis.

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Ketchikan
INDIAN COMMUNITY

RESOLUTION: KIC 19-29

TITLE: **A RESOLUTION OF THE TRIBAL COUNCIL OF THE KETCHIKAN INDIAN COMMUNITY (KIC) TO AUTHORIZE TRIBAL SUPPORT FOR APPLICATION OF NATIONAL ROADLESS RULE ON THE TONGASS NATIONAL FOREST AND TO AUTHORIZE STRONG SUPPORT FOR LASTING PROTECTION OF THE ROADLESS RULE**

WHEREAS, the Ketchikan Indian Community ("KIC or the "Tribe"), is a federally recognized Tribal government organized under a Constitution and Bylaws (collectively, the "Constitution") ratified on October 18, 2017, and previously organized under a Constitution and Bylaws ratified on January 16, 1979, and previously organized under a Constitution and Bylaws ratified on January 27, 1940, in each instance pursuant to Section 16 of the Indian Reorganization Act ("IRA") of 1934 as amended; and

WHEREAS, the KIC Tribal Council (the "Tribal Council") is the representative Tribal Government of the Tribe; and one of the tribe's highest priorities is to protect customary and traditional hunting, fishing, and gathering areas and uses; and

WHEREAS, protection of the inherent right to harvest and use traditional and customary foods requires careful cultural stewardship and protection of the environmental and natural resources; and

WHEREAS, the care of the lands now classified as "inventoried roadless areas" in the Tongass National Forest stretches for millennia; and

WHEREAS, these lands not only provide Alaska Native people with food, they essentially define who we are and where we come from; and

WHEREAS, inventoried roadless areas conserve natural diversity, serve as a bulwark against the spread of invasive species, protect healthy watersheds, and help ensure the continued protection of indigenous fish and wildlife; and

WHEREAS, the Tongass National Forest represents one of the highest carbon stores in the world and conservation of intact inventoried roadless areas on the Tongass is essential for maintaining Alaskan/American resilience to climate change; and

WHEREAS, the Roadless Rule prevents the disturbance of soils and wasteful construction of damaging roads in inventoried roadless areas; and

WHEREAS, according to the State of Alaska, Tongass timber is uncompetitive because of permanent and fundamental changes in global timber markets, high labor costs, distance from markets, and less expensive substitutes; and

WHEREAS, the Tongass timber industry represents less than one percent of jobs and earnings in Southeast Alaska; and

WHEREAS, there are over 5,000 miles of roads already crisscrossing the Tongass National Forest, fragmenting valuable wildlife habitat, threatening salmon by blocking fish passage. And serving as the primary source of sediment into fish streams; and

WHEREAS, spending millions of taxpayer dollars to build roads in inventoried Tongass roadless areas makes no economic sense, particularly given the Forest Service's enormous road maintenance backlog, and

WHEREAS, at hearings held across Southeast Alaska in 2000 on the proposed Roadless Rule, nearly 60 percent of the Southeast Alaskans supported including the Tongass National Forest in the final roadless rule; and

WHEREAS, after the hearing held in Ketchikan during the summer of 2002, the draft supplemental environmental impact prepared to evaluate recommendations for designating additional inventoried roadless areas on the Tongass as "wilderness", the Ketchikan Daily News reported that roughly 85 percent of the public who testified supported more "wilderness";

WHEREAS, the State of Alaska petitioned the USDA to exempt Tongass inventoried roadless areas from the Roadless Rule on January 19, 2018

WHEREAS, for all of the above reasons, the State's petition severely mischaracterizes the actual extent and impacts of the Roadless Rule on Southeast Alaska; and

WHEREAS, the State's petition ignores the fact that the USDA narrowly tailored the Roadless Rule to limit only two activities in roadless areas, road construction, and commercial logging; and

WHEREAS, the State of Alaska's petition ignores the rule's established exceptions, including Federal Aid Highway projects connecting communities, access to mining claims, and logging incidental to otherwise permitted activities, including utility corridors and hydropower projects; and

WHEREAS, on August 2, 2018, the Forest Services signed a memorandum of understanding with the State of Alaska to develop an Alaska-specific roadless rule that addresses management of inventoried roadless areas on the Tongass National Forest; and

WHEREAS, any rule that weakens or eliminates roadless rule protections in what became Inventoried Roadless Areas of the Tongass National Forest will substantially affect the existing 2016 Tongass Land Management Plan Amendment; and

WHEREAS, the 2016 Plan Amendment excluded all roadless areas from the available timber base, the agency's failure to consult and coordinate forest planning with KIC will impair the Tribe's ability to fulfill its responsibility to protect the general welfare and security of tribal citizens; and

WHEREAS, the Forest Service has not explained adequately why it has failed to fulfill its' responsibilities to consult with the Tribe; and

WHEREAS, the State of Alaska resists all efforts to develop and work in a government to government relationship with Tribes and did not consult with KIC before filing petition with the USDA; and

WHEREAS, then Governor Walker appointed a single Alaska Native to the Alaska Roadless Rule Citizens Advisory Committee to represent all tribal perspectives, a gigantic and unrealistic burden for one person; and

WHEREAS, the state and federal governments have demonstrated an unwillingness and an inability to adequately consult, coordinate, and accommodate with tribal interests on the potential implementation of an Alaska-specific roadless rule.

THEREFORE, BE IT RESOLVED THAT, the Forest Service must initiate consultation, coordination and accommodation of tribal interest in any changes to Tongass Land Management Plan connected with this rulemaking process; and

BE IT FURTHER RESOLVED THAT, the only changes to the Roadless Rule that KIC can support is an update to the inventory used to define inventoried roadless areas subject to the Rule on the Tongass to include approximately 350,000 acres excluded from the 1995 inventory used for developing the 2001 Roadless Rule, because the agency assumed approved logging development would occur- when it did not; and

BE IT FURTHER RESOLVED THAT, the Ketchikan Indian Community strongly supports lasting protection for all inventoried roadless areas within the Tongass National Forest as provided in the Roadless Rule.

CERTIFICATION

The foregoing resolution was adopted at a duly convened meeting of the Ketchikan Indian Community Tribal Council, assembled this 15 day of July, 2019 at 2960 Tongass, Ketchikan, Alaska 99901, by a vote of: 8 FOR and Ø AGAINST

N S 7/15/19

Norman Skan, President Date

ATTEST: Gloria Burns 7/15/19

Gloria Burns, Secretary Date

Effective: July 15, 2019 KIC 19-29			
Roll Call	Yes	No	Absent
SKAN			
JOHNSON	X		
BURNS	X		
FRANK	X		
PICKRELL	X		
BENNETT	X		
RAMIREZ	X		
LEASK			
GUTHRIE	X		
WILLIAMS	X		

Review of

Wildlife Management and Conservation Biology

on the

Tongass National Forest:

A Synthesis with Recommendations

A. Ross Kiester

and

Carol Eckhardt

Pacific Northwest Research Station
USDA Forest Service
3200 SW Jefferson Way
Corvallis, OR 97331

March, 1994

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Preface

The Tongass National Forest is not only the largest National Forest, it is one of the most important: it is the best example of temperate coastal rain forest remaining and its well-being is of critical interest not only to the people of southeast Alaska but to all people of the United States and, indeed, the world. Determining the best way to manage this magnificent ecosystem is as difficult a task as the Forest Service has ever undertaken. This review of the Wildlife Management aspects of the Tongass National Forest planning process is intended to help with that task. The review was requested by Regional Forester Michael Barton who asked the Pacific Northwest Research Station to lead the effort independent of any influence from the Alaska Region. PNW Station Director Charles Philpot then asked Ross Kiester of PNW to conduct the review.

Charge to the Review

Regional Forester Barton's request (letter to Station Director, PNW Forest and Range Experiment Station, August 17, 1993) for the review clearly identified a goal:

> Develop the best information available for revising the Tongass Land Management Plan (TLMP) regarding wildlife habitat conservation planning.

In particular:

> The reviews are to determine if the concepts, approaches, assumptions, species information, and conclusions are scientifically sound and if they represent the state of the art in applied conservation biology within the limits of available information.

A critical further consideration is that:

> Your review should be as independent of us in the Alaska Region as possible, in order to ensure the reviews are rigorous and objective.

How the Review was Conducted

To meet this request for an independent review Kiester requested reviews from 18 individual reviewers from across the United States and Canada. In addition, Dr. Carol Eckhardt of PNW was asked to serve as the project coordinator. The reviewers were a mix of people from the Forest Service, universities, and governmental and non-governmental organizations. Without intending at all to slight the many fine scientists in Alaska, we excluded those workers from consideration to maintain independence and to bring a fresh perspective. The three documents to be reviewed were sent to each reviewer

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who then prepared a written review. These 18 reviews are included in this document. During the week of January 17, 1994, Kiester met to discuss the reviews with the reviewers. Kiester and Eckhardt then wrote this synthesis. This document represents our analysis and synthesis of the documents under review and the individual reviews. We are fully responsible for its content. This synthesis is intended to capture the important general points that arose in the individual reviews. It is not intended to duplicate the extensive detail that is contained in those reviews.

Two other activities have contributed to this review. Dr. Eric Forsman provided reviews of the boreal owl and goshawk sections of two of the documents. His review comments are included here. Dr. Andrew Hansen began a project to work with the Tongass National Forest to help expand their GIS modeling efforts. This work is ongoing and will be presented separately.

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Summary of Reviews and Recommendations

We undertook a comprehensive review of three documents produced by the Tongass National Forest wildlife management planning effort. They are:

1. *Appendix M. Fish and Wildlife: A Viability Risk Assessment.*
2. *Habitat Capability Models for Wildlife in Southeast Alaska.*
3. *A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska.*

We obtained 18 individual reviews from wildlife experts of both the United States and Canada. Our synthesis of these 18 individual reviews and our own analysis can be summarized by the following 13 points. The first two points refer to the documents themselves.

1. The documents represent much thought and hard work, but plans are always behind the science on which they are based and their standards are constantly being raised.

2. Overall the *Strategy* gets high marks, *Appendix M* is not as thorough or well motivated, and *Models* requires rethinking. None of the planning alternatives described or suggested is adequate at this time to ensure viability of all species.

The rest of the points are recommendations for the planning process.

3. Recognize the global significance of the Tongass National Forest.

4. Understand the implications of insularity and topography for natural fragmentation: the Tongass National Forest is naturally significantly fragmented and any management-induced fragmentation must be evaluated in this context.

5. Evaluate and synthesize additional methods beyond the Management Indicator Species method:

1. Population Viability Analysis.
2. GAP Analysis.
3. Evolution/Genetic Analysis.

6. Within the Management Indicator Species method:

1. Add more species.
2. Obtain data specific to populations on the Tongass National Forest.

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7. Evaluate and synthesize additional landscape approaches to the Habitat Conservation Area including:

1. Inverse of the Habitat Conservation Area.
2. Large reserves.

8. Within the Habitat Conservation Areas approach:

1. Define precisely the rules for use.
2. Do not log or build roads within them.
3. Design in three dimensions.
4. Factor in the effects of all other habitats.

9. Move beyond the habitat capability models to develop closer approximations to spatially explicit Population Viability Analyses.

10. Immediate Recommendation: Keep Landscape options open.

1. Do not further fragment existing large blocks of high volume old-growth.
2. Do not differentially cut low altitude, high volume old-growth.

11. Short-term Recommendation: Initiate a 5-pronged short-term research and data acquisition effort:

1. Do complete Population Viability Analysis for a large species (brown bear).
2. Do an evolutionary analysis for a small species group (deer mice or voles).
3. Construct a three-dimensional "photograph" of the current physical and biological environment of the Tongass National Forest.
4. Learn about regeneration and second-growth wildlife relations.
5. Initiate a biological survey.

12. Long-term Recommendation: Implement adaptive ecosystem management.

1. Create a planning process for adaptive ecosystem management.
2. Plan using natural patterns of disturbance as a guide.
3. Synthesize species-based and landscape-based approaches.

13. Build on interagency approach and consider international coordination.

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1 Introduction

Scientific progress is continuous while final management plans are issued only at intervals. Therefore, we must expect that there will always be something of a discontinuity between the two. In addition, it is also the case that the standards for National Forest Plans have been continually raised in the last few years. This "raising of the bar" virtually guarantees that any planning document more than a few years old will be out of date. Therefore, no particularly useful purpose is served by dissecting older work. Rather, we recognize that a tremendous amount of work has gone into previous planning efforts for the Tongass National Forest and that our contribution is best made by indicating how to build on previous work and move forward with the creation of a new plan.

1.1 Challenges of the Review

This review of the wildlife management portion of the Tongass Land Management Plan (TLMP) is made especially challenging by the following three factors:

1.1.1 Part of a Plan

We dealt only with three documents that were relevant to wildlife management and conservation biology. These constitute only a small fraction of the Tongass National Forest planning effort. However, issues such as silvicultural prescription, stand growth and yield, harvesting models, recreation, and hunting (both subsistence and recreational) all affect wildlife in complex ways. It is therefore not possible to give as comprehensive a review as we would desire in the absence of this information. On the other hand, reviewing an entire plan would be a monumental task, requiring a great deal more effort but producing a correspondingly more valuable review.

1.1.2 Other Ongoing Reviews

Our effort is not the only review currently being conducted on the Tongass National Forest that could impinge on our results. The PACFISH effort to look at anadromous fish and their habitats overlaps our effort in riparian areas. Two species (goshawk and marbled murrelet) have recently been proposed for listing under the Endangered Species Act and efforts here are directly relevant to other wildlife. Finally, it is by no means the case that the Alaska Region has been idle while we did our work. New ideas and information are coming in as we write.

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1.1.3 What is Ecosystem Management?

It is now Forest Service policy that National Forests should implement Ecosystem Management. But it is far from clear what this means, especially in an operational sense. The Forest Service is in the middle of a revolution of ideas in both science and management whose outcome is yet to be determined. Every National Forest is struggling to understand what could be meant by Ecosystem Management and the Tongass National Forest is no exception. The challenge to us and the individual reviewers was to place wildlife management and conservation biology in the context of a vision of ecosystem management.

1.2 Focus on Three Documents

Our review specifically covered three documents that have been developed as part of the TLMP process:

1. *Appendix M. Fish and Wildlife: A Viability Risk Assessment.* This document is by the Tongass Land Management Planning Team and is an Appendix to the Draft Environmental Impact Statement. (Abbreviated as "*Appendix M*")

2. *Habitat Capability Models for Wildlife in Southeast Alaska.* This document was compiled by Lowell Suring. Each species model has separate authors. (Abbreviated as "*Models*")

3. *A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska. Report of An Interagency Committee.* Lowell Suring chaired this committee which included representatives of the Forest Service, the Fish and Wildlife Service, and the Alaska Department of Fish and Game. (Abbreviated as "*Strategy*")

1.3 Road Map for the Synthesis

In what follows we first give a short evaluation of the three documents as such. We then proceed to a review of the background and general concepts of wildlife management and conservation biology. We then review each species selected by the Region as a Management Indicator Species (MIS) for which we had comments. We follow with a series of recommendations for the planning process, data collection, management, and monitoring. Finally, we discuss directions for follow-up to this review.

We did not undertake separate reviews of *Models*, rather all three documents were reviewed by all individual reviewers. Different individual reviews focused on particular species in *Models* and *Strategy* that they were familiar with.

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2 Evaluation of the Three Documents

In this Section we give a short evaluation of each of the three documents. Details are given in the rest of the Synthesis which considers each of the documents as necessary.

2.1 *Appendix M*

The risk-based approach taken by *Appendix M* is a good beginning, especially given the limited data available. However, the documents need more to be credible and must go further to meet the requirements of the relevant legislation. In particular criteria for the selection of Management Indicator Species need to be made clear, and alternative methods of analysis need to be included. None of the planning alternatives currently considered is adequate to ensure viability of all of the species considered.

2.2 *Strategy*

Overall the *Strategy* receives high marks. It represents a solid attempt to integrate species viability concerns with the Habitat Conservation Area approach. It demonstrates a good awareness of modern concepts of wildlife management and conservation biology. However, it needs to consider other methods and approaches besides Habitat Conservation Areas as well. The particular pattern of Habitat Conservation Areas that it suggests will not ensure viability of all species.

2.3 *Models*

The Habitat Capability Models are a good organizing tool for understanding individual species. However, most of the specific models suffer from a lack of data and none has any calculation of the probable error associated with them. This modeling approach needs to be rethought and a program of work to develop them into models that have Tongass-specific data and confidence limits needs to be developed. The individual species models vary considerably in the amount of relevant biology and data that they contain. Some are in good enough shape to provide the basis for a Population Viability Analysis in the near future while others have much further to go.

3 Background

3.1 Ecological Background and Context

3.1.1 Global Distribution of Temperate Coastal Rain Forest

The Tongass National Forest may be classified as belonging to the Coastal Temperate Rain Forest Biome. This biome was never common over the

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earth's surface occupying only 30-40 million hectares in preindustrial times. Today only about half of that remains forested. The Tongass National Forest contains 14% of the world's total acreage and 29% of the remaining unlogged acreage (Table 1). These estimates from Weigand (1990) and Conservation International (1992) are quite rough. Nonetheless, it is clear that the Tongass National Forest has as important a place in the world's ranking of forests as any. These figures are the basis of much of the national and international attention that has come to be focused on the Tongass National Forest.

Table 1

Acres of Coastal Temperate Rain Forest

	Total	Unlogged
World	65,735,536	28,541,861
Alaska	12,274,532	10,761,092
Tongass NF	8,981,998	8,225,198

3.1.2 History of the Tongass National Forest

By most standards the Tongass National Forest is a young forest having come into existence about 10,000 years ago as the glaciers receded. During the Vashon Maximum (20K to 14K years Before Present), the Cordilleran Ice Sheet in the Pacific area extended to the north end of the Olympic Peninsula and along the Puget lowlands covering what is now the Tongass National Forest. Then, a time of extensive ice recession began around 14.5K years BP when lowlands became ice-free and could serve as coastal refugia. Glacial ice in southeast Alaska receded about 10,000 years ago and the islands of the Alexander Archipelago were apparently free of ice for at least a few hundred years before the mainland. Palynological studies suggest that land areas freed of ice became vegetated rapidly with alder, ferns, sedges, and willows. Lodgepole pine was the first dominant tree to colonize the Alexander Archipelago, followed by Sitka spruce, mountain hemlock, and recently western hemlock (Ritchie, 1987). Pollen records further indicate that there was clear division into pre- and post-10K-yr-BP time periods with a change from the dominance of Pseudotsuga to a later dominance of Cupressaceae and western hemlock. Other species, particularly of *Alnus*, *Abies*, and *Pteridium*, also increased after the 10K-yr-BP mark. At about 7.5K yr BP, closed-canopy forests of Pseudotsuga, lodgepole pine, *Picea*, and *Betula* spread and open vegetation declined. More recently, "increases in *Picea* and *Abies* (slight) at 4.7K yr BP signal

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the establishment of the modern, presettlement vegetation ..." (Ritchie, 1987:114). Along the southern Alaska coastal strip (the North Pacific Zone), the early *Alnus-Pinus* contorta-Cyperaceae assemblage (10K yr BP) was replaced by a succession of Sitka spruce, western hemlock, and mountain hemlock to form the modern configuration of forests by the late Holocene (Ritchie, 1987).

3.1.3 Natural Fragmentation

From a wildlife point of view the most important fact about the Tongass National Forest is that it is an archipelago: it is made up of very many islands of different sizes and of different distances from each other. This dominant feature sets the stage for all other factors that affect wildlife. The way that the island structure affects a species is dependent on the dispersal capability of the species and thus roughly on body size. For large species such as bears, the island structure is a challenge for dispersal and can be considered as driving metapopulation dynamics. For small species such as mice, island structure provides the evolutionary opportunity for local adaptation and in some cases speciation. Any plan that does not adequately consider these effects will not be biologically realistic over the periods of time implied by a long rotation.

The extraordinary topographic relief of much of the Tongass National Forest is the second feature of the landscape that exerts a major effect on wildlife. In particular, the dendritic pattern of forests as they extend up valleys in steep areas creates a high degree of fragmentation. This is because the routes of dispersal that an animal must take are much longer than the "as the crow flies" distance. The intervening rock, ice, and tundra cannot serve as dispersal routes for many species except for some birds.

Taken together the island structure and the dendritic pattern of much of the forest means that the Tongass National Forest has a natural level of fragmentation unsurpassed by any other National Forest. It is, of course, the only National Forest that is largely an oceanic archipelago. This base level of fragmentation must be clearly understood before the effects of management-induced fragmentation can be properly evaluated.

The effect of this natural fragmentation on a given species depends on individual species' dispersal abilities and, for non-birds, that ability is strongly related to body size. For large animals such as bears and wolves which have good dispersal capability (they can travel long distances and even swim) the fragmentation simply presents a series of dispersal obstacles to be overcome. For them fragmentation is important in that it affects metapopulation dynamics. Small species on the other hand are often nearly completely prevented from dispersing between islands and isolated watersheds so that fragmentation provides the evolutionary

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opportunity to evolve local adaptation. We see this in the many subspecies that have been described for small mammals on the Tongass National Forest. Figure 1 shows this idea graphically and describes the range of effects that fragmentation can have as a function of body size. Clearly birds must be considered differently; their exact dispersal abilities would have to be known to place them on the graph.

Scaling the Effect of Fragmentation

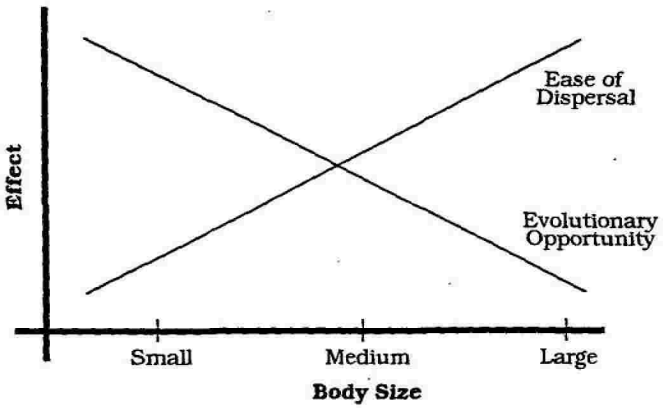

Figure 1: The Effect of Fragmentation Depends Upon Body Size

3.2 Legal and Management Background and Context

There are four key pieces of legislation that are relevant to wildlife and conservation on the Tongass National Forest:

1. National Environmental Protection Act (NEPA)
2. Endangered Species Act (ESA)
3. National Forest Management Act (NFMA)
4. Tongass Timber Reform Act (TTRA)

Taken together these acts and their antecedents provide the legal authority for management of wildlife and biodiversity. They are supplemented by Forest Service Regulations which have a similar legal status to the acts themselves.

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The most important aspect of these acts and regulations for our purposes are the requirements for viable populations and for the prevention of extinction. The plan for management must thoroughly address these issues. The acts and regulations also provide for consideration of biodiversity in general, but the requirements for management are less strict.

Proceeding on a species by species basis to establish viability is not usually workable because of the amount of information required. However, NEPA, ESA and NFMA provide the authority to plan for forest management on a broad, ecosystem basis, and require full consideration of this approach at least as an alternative management strategy. This conclusion was also reached by the Forest Ecosystem Management Team (FEMAT, 1993) which concluded that the species viability approach and the ecosystem-based approach were complementary and that both should be implemented.

An important area of the law that is evolving concerns legal requirements for planning in the absence of data. We believe that an argument can be made that places the burden of proof of no adverse impact on the viability of populations on the plan.

3.3 Philosophical Bases for Wildlife Management and Conservation

3.3.1 Values

No scientist is free of values so it is important to state up front that we believe wildlife is an important part of our life and heritage. Within that broad belief we seek to understand the ecology of species and their communities so that they may be perpetuated indefinitely.

3.3.2 Paradigms

Wildlife biology and conservation biology are currently very active disciplines and therefore many approaches often exist to attack a given problem. In the process of synthesizing this review we were often able to conclude that alternative paradigms should be investigated, rather than deciding that there was one best way to do things. Indeed, under one vision of ecosystem management the concept of "best practice" is seen to disappear and be replaced by a system of testing and evaluating alternatives (Bormann *et al.*, 1994).

However, over the last few years a clear trend in wildlife management and conservation biology has been to move forward from a few indicator species in two directions. First, more species are considered leading ultimately to the GAP Analysis approach which considers all vertebrate species. Second, methods of analysis of higher order ecological entities such as communities, ecosystems, and landscapes have become well-developed.

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We believe that the future holds a synthesis of these two approaches. Individual species viability analyses and community/landscape analyses will be combined in a dynamic, spatially explicit approach.

3.3.3 Options and Trade-offs

In the exploitation of the forest there are often trade-offs. These may be between different aspects of the forest or between different sectors of the economy or both. These trade-offs have only rarely been made explicit as, for example, in the FEMAT process (FEMAT, 1993). In this review we analyze wildlife and biodiversity, but the explicit delineation of the trade-offs between wildlife and other activities must be made in the context of the entire plan.

Each planning option implies certain trade-offs. In order to understand how this relationship works it is important to develop a no timber harvest option for wildlife as a baseline to which the other options may be compared. This was done in the FEMAT (1993) process as Option 1. We strongly recommend development of such a wildlife baseline option for the Tongass National Forest.

4 General Review

Overall the vision that must be built for wildlife on the Tongass National Forest must consider the following principles:

4.1 The World is Stochastic.

The population dynamics of any species will inevitably contain an important and sometimes dominating random component. Even with massive amounts of data, predicting the future trajectory of a population can be virtually impossible. Many environmental effects on habitats and populations occur at random as well. Management and planning must be done with a full understanding of the limits of prediction at different scales. This idea is one the fundamental principles of ecosystem management according to Bormann *et al.* (1994).

Within the specific context of population viability analysis it is now generally recognized that demographic and environmental stochasticity together with random catastrophes are the major factors determining the probability of persistence of a population (Shaffer, 1981; Lande, 1993). Thus these factors must be carefully considered in any population viability analysis.

These stochastic influences on population dynamics imply that we must exercise extreme caution in choosing a minimum viable population as a

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management target. Because of stochastic effects a minimum must be larger than one would expect from a simple deterministic model. In particular, the minima suggested by the Habitat Capability Model approach are too small.

4.2 Species Populations are Interactive and Not Always Positively Correlated.

Populations of predators and prey are sometimes negatively correlated with each other and many species compete in a way that lowers each other's populations. As an example we find that the black bear and brown bear occupy mutually exclusive islands within the Tongass National Forest. Other, less dramatic, interactions abound.

4.3 Population Dynamics and Interactions are Scale-dependent.

Species differ greatly in the degree to which local populations are synchronous with each other. Because of this, metapopulation dynamics rarely coincides with the dynamics of a single population and the dynamics at a larger scale must be considered. In particular, some populations may be sources of individuals moving into other populations which may be sinks. The pattern of sources and sinks may change through time and it is this pattern which may determine overall viability (Pulliam and Danielson, 1991).

4.4 Landscape Effects

Many species utilize, or may require, more than one kind of community, and the way communities are arranged spatially can affect the viability of populations. For example, the Tongass National Forest brown bears require on an annual basis old-growth forest juxtaposed to a salmon stream.

5 Multiple Paradigms

Viability requirements are the strongest legal mandate for management. However, there is no single way to approach guaranteeing viability. The FEMAT (1993) process concluded that species-based and landscape-based approaches are both biologically sound and legal. Below we list several approaches of both types that must be considered for the Tongass National Forest. These approaches are by no means mutually exclusive and it will be a synthesis of these approaches appropriate for the Tongass National Forest that must be created for the planning effort.

5.1 Management Indicator Species (MIS) Approach

The MIS approach is the primary method adopted by all three documents. In this approach, a relatively small group of species is chosen and the assumption is made that if these species populations are made viable and

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well-distributed that the other species in the old-growth forest will also do well. Below we discuss the implementation of this paradigm in detail.

5.1.1 Strengths and Weaknesses

The strength or weakness of a given set of MIS depends on what the MIS indicate. In general, populations of a given species will be well correlated with many others only when environmental degradation is severe. If a habitat is altered enough, all species within it will decrease and any one species will be as good an indicator as another. Where change is not severe, any one species will be well correlated with only a few others and may be negatively correlated with several others. In these cases the details of population interactions can dominate the dynamics and obscure the value of the MIS.

In particular, any approach which assumes that the habitat of only a few species is also the habitat of many other species is not workable. For example, the FEMAT process (FEMAT, 1993) found that the habitats of only very few other species were approximated by the habitat of the spotted owl.

The strength of the MIS method lies in the orderly analysis of the information that we do have about better known species. The process of selecting a suite of MIS and undertaking a summary and analysis of those species inevitably will lead to a clearer picture of the issues and data needs that the planner must face.

5.1.2 Methods of Choosing Species

The methods of choosing the MIS differed between *Appendix M* and the *Strategy*. The list of species chosen by the authors of *Appendix M* was not biologically well-motivated or representative and is an important flaw in that document. The authors of the *Strategy* undertook a selection process which involved deciding on several criteria, assigning importance values to the criteria, and applying those values to all vertebrate species. While the criteria themselves could be debated, the overall method is an important advance. Lack of data hampered the *Strategy* from achieving the kinds of analysis that might have been desired such as that done by Millsap *et al.* (1990) for the vertebrates of Florida. In particular, lack of knowledge of population spatial patterns and dynamics is a problem. In general, the criteria for selection of species should reflect the reliability of those species to be truly representative of the communities of which they are a component.

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5.1.3 MIS Chosen

Given the differences in the method of choosing MIS it is perhaps not surprising that *Appendix M* and the *Strategy* produced different lists of species on which to focus attention. These two lists are given in Table 2. These species will be considered individually in Section 6.

Table 2.
Species Lists

Appendix M and *Models*	*Strategy*
Black Bear	
Blue Grouse	
Red Squirrel	
Sitka Black-tailed Deer	
Brown Creeper	
Red-breasted Sapsucker	
Hairy Woodpecker	
Bald Eagle	
Vancouver Canada Goose	
Gray Wolf	Gray Wolf
Brown Bear	Brown Bear
Marten	Marten
River Otter	River Otter
Mountain Goat	Mountain Goat
	Northern Goshawk
	Boreal Owl
	Northern Flying Squirrel
	Great Blue Heron

5.1.4 Species Not Chosen

Obviously many more species were not chosen as MIS than were chosen. Many of the species that were chosen are good MIS while a few may not be. Evaluations of the species chosen as MIS are given in Section 6. Some species that live on the Tongass National Forest but were not deemed to be associated with old-growth forest may be worth reconsidering (e.g., wood frog). Here we discuss some species or groups that were not chosen.

Amphibians. No species of amphibians were included. They are usually considered good potential indicators of environmental quality because they span aquatic and terrestrial systems, are herbivorous as tadpole and

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carnivorous as adults, have a skin that is relatively permeable subjecting them to direct chemical effects, and are relatively easy to monitor because they aggregate for breeding. The spotted frog (*Rana pretiosa*) and the western toad (*Bufo boreas*) are candidates for MIS based on these criteria (Waters, 1992).

Birds. Other species of birds should be considered. The crossbill species complex that is on the Tongass National Forest is currently taxonomically problematic and for that reason in need of attention. One putative species of crossbill (and possibly another) is specialized on a single species of conifer in the Tongass National Forest. All crossbills are very sensitive to conifer seed crops and thus are good indicators of old-growth. Vaux's swift, varied thrush, and harlequin duck are three additional species that could provide important information. Vaux's swift is dependent on old-growth for nesting, varied thrush is easy to monitor and closely tied to old-growth, and the harlequin duck uses riparian areas within old-growth.

Mammals. The ermine occurs on the Tongass National Forest and has differentiated evolutionarily. It would provide an example of a medium-sized mammal species, but it is known that its populations fluctuate greatly so it would be a difficult species to monitor. Concerns about marine mammals were dismissed without discussion in *Appendix M* and we wonder if that dismissal is supportable.

Non-vertebrates. While invertebrates and understory plant species are not themselves considered to have the same status as vertebrates, it may well be the case that they would be better indicators of environmental quality than vertebrates. Some are also direct indicators of the vertebrates themselves. For example, conifer seed production is crucial to several birds and mammals and could be monitored relatively easily especially in relation to stand age and composition.

In addition, the Forest Service does have regulations about Threatened, Endangered, and Sensitive species including invertebrates and plants and planning efforts regarding these species need to be more fully integrated with the wildlife planning.

5.1.5 Habitat Capability Models in General

Models contains Habitat Capability Models (HCMs) for 14 species. The individual species models are discussed in Section 6. Here we make some general comments on HCMs. We have a good deal of reservation about the HCMs. The greatest concern is about the false precision that the models imply. They may be precise, but the accuracy is unknown and we assume it to be very low. The models are deterministic and do not take into account any stochastic features of the relationship between habitat and population

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and they are parameterized with data whose error limits are unknown and likely very high. Thus the confidence limits for the models, were they to be calculated in some way, would surely be so large as to render the models close to useless. Also, as the authors of *Models* point out, the models may be quite sensitive to small changes in parameter values in ways that are not understood. Moreover, these models do not, in general, incorporate interactions with species not included in the habitat description itself, nor do they take into account a species' use and possible dependency on required habitat juxtapositions. So, there are both parametric and structural uncertainties.

These models have played a useful role in organizing current knowledge and emphasizing knowledge gaps, but it is now time to build on this beginning and move to more realistic approaches whose confidence limits can be calculated. We discuss other modeling approaches in the recommendations.

As an aside, if the HCMs are to be developed further they should be recoded into a more general form and produced in a language that would allow sensitivity analyses. INFO does not lend itself to clarity of expression or to developing code that will be run many thousands of times as would be the case in a Monte Carlo sensitivity analysis.

5.2 Population Viability Analysis (PVA) Approach

PVA is now a standard tool in conservation biology and represents the most sophisticated approach to estimating the viability of single species. It provides a detailed model of the factors affecting a species and of its current situation and likely dynamics. In an ideal world a PVA would be desirable for each species of concern. However, constructing a PVA is time consuming and data intensive so that realistically only very few species can be done. Nonetheless, we feel this approach should be tried for at least one species on the Tongass National Forest (the brown bear, see Section 7.4.1).

The Habitat Capability Models of *Models* can be viewed as a start towards PVAs for the species modeled. Further work undertaken on those models should be done in such a way as to more closely approximate PVAs for those species.

5.3 Landscape Design Approach

5.3.1 Introduction

Conservation biology is replete with theory and guidelines for what may be called the landscape design approach to managing wildlife and biodiversity. In any real world case, constraints of the actual pattern of the

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landscape that are available to start with may severely limit the options. Each of the approaches discussed below must be examined for its own merits and how it fits into the existing pattern of landscape on the Tongass National Forest. As with the overall approaches, these alternatives are not mutually exclusive and the challenge for the Tongass National Forest is to synthesize them in a way appropriate for that forest.

5.3.2 Habitat Conservation Area (HCA) Paradigm

The HCA paradigm has been developed most thoroughly for the spotted owl in the Pacific Northwest. Here the landscape is severely fragmented, but the owl has long distance dispersal abilities. It is a plausible (if, untested in practice) approach for that species in that environment, but will be less successful for species whose biology and distribution are different. In particular, species that have difficulty dispersing may not be viable as a metapopulation. Large species such as brown bear and wolf may require individual HCAs that are quite large to maintain populations within the HCAs. For many species the nature of all other habitats, including second-growth, that are not in HCAs in which the HCAs are embedded may be crucial. Finally, it may not be the best paradigm for the Tongass National Forest which is less fragmented from logging, but more fragmented naturally than the Pacific Northwest and where other options still exist.

If the HCA paradigm is used as part of a landscape design strategy, it is very important that the rules of use within the HCAs be carefully specified. The *Strategy* is not as clear on this topic as it could be. In particular, no logging or further road building should be undertaken in HCAs. Hunting in HCAs is a difficult issue. It should only be done where it clearly does not conflict with the primary purpose of the HCA to maintain viable populations.

5.3.3 Inverse of HCA Paradigm

For species with limited dispersal ability, the most appropriate landscape structure may be to harvest timber in isolated patches and manage the rest for old-growth species. There is no *a priori* reason that either wildlife or logging should be in reserves. This approach would produce a pattern that is a "photographic negative" of the HCA pattern. That is, instead of having reserves for the protection of wildlife, reserves for logging are created.

5.3.4 Corridors and "Pinch Points"

The design of a system of dispersal corridors is a necessary complement to most other paradigms. The issue of corridor width is prominent in the discussion of several species. In particular, the marten requires wider

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corridors than are used in the *Strategy*. Some corridors are unique connections between areas and the "pinch points" (corridors which are the only connection between two areas that when connected make up an important landscape network) must be carefully protected. The determination of pinch points comes when a general corridor design is implemented over a landscape with a preexisting pattern of fragmentation.

Corridors on the Tongass National Forest must be designed with full consideration of the topography that they cover. The extreme topographic relief of much of the Tongass National Forest means that landscape planning must occur in three dimensions.

Corridors obviously are not independent of the landscape components they connect. They will be important, however, in any comprehensive landscape design. Unfortunately, it is worth remembering that corridors are virtually untested in practice.

5.3.5 Second-Growth and Regeneration Issues

The HCA, inverse HCA, and corridors approaches all beg the question of the nature of the second-growth forest. The amount, kind and spatial distribution of second-growth depends on the patterns of regeneration that occur on the Tongass National Forest. These patterns of regeneration are only poorly understood at this time and yet will be crucial to any landscape design strategy (see Section 7.4.4). This is an important point where wildlife considerations interact with other parts of the planning effort. Silviculture and harvesting methods will dictate much of the future pattern of second-growth.

5.3.6 Large Reserves Paradigm

Consideration of the brown bear and wolf lead to the necessity of examining a system of large reserves to accommodate viable populations of the species. Such a system would also provide for the viability of many other species as well. The possibilities of this approach should be examined both in terms of the potential sites available and the degree to which these sites could support most other species of concern.

5.3.7 Rotating Block Timber Harvesting

Because of the unusually long time needed for succession to achieve climax in these temperate rain forests, a rotating block design for timber harvesting is not appropriate. Therefore, sufficient biodiversity reserves must be established, and these must be permanently unavailable for timber harvest. Otherwise blocks must be allowed to serve as source areas for many years beyond the age at rotation.

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5.4 GAP Biodiversity Approach

GAP Analysis (Scott *et al.*, 1993, and references therein) is an approach that considers all vertebrate species and vegetation classes. The principal motivation for GAP Analysis is to identify species that may become inviable before they are in serious trouble thereby making their management a much less expensive undertaking. GAP Analysis proceeds by first making a vegetation cover type map (the national standard is for a 100-hectare minimum mapping unit). A wildlife habitat relation model associating each species to the appropriate vegetation cover types is then constructed. Known occurrences of each species are then used to identify appropriate vegetation polygons within a radius of extrapolation. This produces a detailed model of the range of each species. These ranges are then combined to produce maps of species richness. Finally these maps are overlaid on maps of land management systems. Species that do not have significant occurrences within areas managed for the long-term protection of biodiversity (e.g., wilderness areas) are then identified as a "gap" in the protection of biodiversity and become candidates for further management action. In theory Gap Analysis can be run "in reverse" to identify those areas which are least important to the maintenance of species as well.

The GAP Analysis Program was developed within the Fish and Wildlife Service with literally hundreds of cooperators. It is now part of the National Biological Survey within the Department of Interior. The GAP Program is active in over 30 states and will begin in Alaska within two years. The Tongass National Forest should consider this methodology and become an initial cooperator with the Alaska GAP program.

5.5 Island Evolution Approach

Many species of vertebrates on the Tongass National Forest have undergone extensive local evolution because of isolation and local adaptation. Several species have described subspecies and some isolates are customarily regarded as full species (e.g., *Microtus coronarius*). The true extent of local genetic variation among the smaller species on the Tongass National Forest is unknown at this time. Mapping the patterns of genetic differentiation between islands and isolated watersheds is the first step. This activity will reveal those areas that contain novel genetic variation. These areas most likely will prove to be small islands and watersheds isolated by topography from other watersheds. The overall effect is similar to the evolution of different stocks of salmon endemic to particular river systems and these patterns of genetic differentiation among small terrestrial animals will present similar management challenges.

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5.6 The Future: A Dynamic Synthesis

We wish that we could say that a synthesis of all of the approaches above has been completed and could be directly applied to the Tongass National Forest, but this is simply not yet the case. Nonetheless we believe that the Tongass National Forest is in a good position to rise to the challenge of creating such a synthesis. The work done so far and the GIS databases that have already been created provide the beginning for a dynamic, spatially explicit modeling framework. This framework would be the synthesis needed to bring the general concepts outlined here down to the specific realities of the Tongass National Forest.

6 Species Accounts and Recommendations

Here we summarize the species specific reviews and recommendations for the 18 species listed in Table 2. In this Section we refer to the authors of the individual reviews that cover a given species.

6.1 Vancouver Canada Goose

Jarvis and Ratti specifically address the sections of the plan that pertain to Vancouver Canada Goose. Of particular concern is the narrow definition of factors that impinge on this species. The Habitat Capability Model is primarily based on conditions for nesting and brooding. Most ecologists now understand the importance of winter habitat in determining body condition prior to breeding and nesting. The reviewers also express concern for the lack of depth and selectivity in the literature review that supports this section of the plan. The Pacific Flyway management plan and recent research on migration and wintering should be referenced as important supporting information on this species. Both reviewers also maintain that the model's focus on *Vaccinium* as an indicator of habitat for Vancouver Canada geese is too limiting. Jarvis particularly points out that tree canopy cover could be important. Presence or absence of bears may also be a critical variable. The Habitat Capability Model for the Vancouver Canada goose is regarded by the reviewers as too narrowly defined and based on outdated perceptions of the needs of this species.

6.2 Bald Eagle

The bald eagle has been the subject of a great deal of research generally, and particularly, on the Tongass National Forest. Hansen refers to a U.S. Fish and Wildlife Service data set that would have provided pertinent information for the model. Topographic information is especially relevant to evaluating breeding and nesting habitat. Hansen also questions predicting eagle density based on habitat capability rather than the availability of food resources. An additional problem arises from the assumption that eagle density can be

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predicted by using a ratio of breeding to non-breeding adults based on nesting habitat. Hansen indicates that non-breeding adults do not use the same kind of habitat that breeding adults do. Generally, Hansen found the Bald Eagle model, as it appears, to be "inadequate" at best, and potentially misleading. He offers the following recommendations: 1. Use the US Fish and Wildlife Service data for the basis of a revised habitat capability model for the bald eagle. These data should be used for the individual provinces to provide valid, local information. 2. Standards and guidelines should be based both on actual field information as well as projected habitat suitability. 3. Designated habitats should be monitored for effectiveness. 4. Annual monitoring information should inform planners as to the effectiveness of the planning and to understand changes in abundance of eagles, food sources, and reproductive success.

6.3 Hairy Woodpecker

The choice of the hairy woodpecker as a management indicator species was regarded as appropriate by Walters in that it requires a very specific microhabitat which, when present, assures associated habitat for other species as well.

6.4 Red-breasted Sapsucker

Walters indicates that this species is important to the community as a cavity excavator and thus a good choice for an MIS. However, previous work indicates that woodpeckers populations are limited by winter factors. This conclusion severely restricts the applicability of a model based on breeding season only.

6.5 Brown Creeper

Walters supports the choice of the brown creeper as an indicator species. He references several sources that validate the relationship of brown creepers to old-growth forests. Although it may be inferred that the species would be vulnerable to disturbance of old-growth habitat, Walters cites a serious lack of data, both for baseline data and replication studies to better inform the modeling efforts.

6.6 Gray Wolf

Several reviewers provide perspectives on the gray wolf. Paquet points out that, while the viability risk assessment, species account and strategies are likely to be adequate, they are based on less than current research. He also states that several factors militate against the goal of maintaining a large enough wolf population for long-term sustainability. The major factor is that the Tongass National Forest does not provide enough viable habitat within its

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own boundaries. Cooperative efforts between the Tongass National Forest, the State of Alaska and the federal and provincial governments of Canada are necessary to accommodate the territorial needs of wolves. Given the extreme topography of much of the Tongass National Forest, much available wolf habitat will be restricted to lower valleys that are also optimum acreage for timber harvest. Both Paquet and Pletscher indicate concern that modeling and planning were based on limited and outdated information. The habitat capability model for the wolf is seriously lacking in that it neglects factors that may be vitally relevant such as the impact of road density, competition with other species for prey, and seasonal effects on the distribution, weights and values of prey. Shaffer expresses concern about the adequacy of second-growth forest as habitat for wolf prey. Shaffer also points out that viability for wolves is of more concern than some other species because of "...their much lower density and...susceptibility to human induced mortality." Lidicker questions the expectation of a 14.6% annual harvest of the gray wolf population which is legally protected.

6.7 Black Bear

Relatively little is known about the black bear and McLellan expresses concern about the number of habitat classes in the black and brown bear models. He notes that there are only 2 classes for the brown bear, about which more is known, but 32 classes for the black bear. These differences are not explained. McLellan also recommends incorporating additional factors in the black and brown bear models such as clear-cuts versus alternative harvesting, herbicide applications, burning, and agriculture. Interactions with brown bears should be included.

6.8 Brown Bear

The brown bear sections of the *Strategy* are regarded by McLellan as well-done and based on respected research. He has concerns about the density calculations, and nutritional factors for females lactating in spring. The survival of brown bears, and many other species as well, is complicated by interaction with humans. This is especially true for bears given impacts of timber harvest that translate to three basic types: habitat change, displacement, and mortality. Shaffer found the "quantitative population viability assessment for the brown bear is too simplistic to give me much confidence. We know what the impacts of proposed management will mean for the survival of that species on this forest." McLellan and Shaffer agree that this species is a good candidate for a complete Population Viability Analysis. Interactions with black bears should be included as well.

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6.9 Marten

Several of the reviewers express concern about whether martens would use corridors in the HCA model. Benkman states that the distance of 40 km between large HCAs was chosen because it is near the maximum dispersal distance recorded for martens. Martens are also known to avoid crossing clear-cuts. Powell questions the assertion that martens do not use high elevations in southeast Alaska since in the Rocky Mountains and Pacific Northwest they use high but not low elevations. Another issue is the operational definition of a "reproductive unit" for martens. Powell discredits any planning or decision making based on this concept for martens. The specifications for spacing and size of HCAs does not appear to be realistic for the needs of martens, particularly during years when prey populations are low. It cannot be assumed that the animals will know which direction to proceed when leaving an area so as to be successful in reaching another, more viable area for sources of prey and mating.

6.10 River Otter

Powell notes that since habitat for otters is essentially linear, conversion to area measures is inappropriate.

6.11 Sitka Black-tailed Deer

The quality and amount of research supporting the model for the black-tailed deer is impressive and complimented by McCullough. The sampling and analysis techniques used to verify the model are problematic in that there is not enough methodological information available on which to evaluate the analyses. Other concerns relate to the type of variables included in the analyses. Some are short-term in effect such as snowfall, hunting, and predators. Others such as logging, forest fragmentation, and successional stage are long-term processes which manifest in much different ways. An additional concern addresses the issue of using a mean value for snowfall throughout the forest when there is considerable variation from northern to southern regions of the forest. The model needs to incorporate these issues in order to provide a realistic assessment of the habitat. The HCA model for maintaining viable populations of Sitka black-tailed deer on the Tongass National Forest is probably not suitable for the long term. McCullough expresses concerns that problems of oscillating factors may create extremes in population that would make the deer especially vulnerable to the pressures of hunting and wolf predation. This combination of factors could place the viability of the species in question. There appears to be adequate research in place for the Sitka black-tailed deer. Research efforts could be directed at other species for which less is known. However, research on monitoring of deer population levels should be conducted.

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6.12 Mountain Goat

A problem in logic is apparent in the discussion of the mountain goat in that a population of 50 is defined as minimally viable but that areas supporting more animals should be managed to support at least 50 rather than some larger number. Moreover, the recommendations are derived from a study on mountain sheep and generalizations made to mountain goats. A critical point for the mountain goat population depends on whether or not they are isolated by habitat fragmentation.

6.13 Red Squirrel

Red squirrels may serve well as a management indicator species given their vocal and diurnal habits. Smith reports that they also tend to use the same cache sites for cones for several years. Smith indicates that the Habitat Capability Model for red squirrels is probably suitable during periods when food sources are adequate. However, in years when the seed crop in Sitka spruce and western hemlock fails, the squirrels have to emigrate to other areas with less abundant food supply. This issue becomes especially critical considering that seed production in these species of trees is affected by climatic variations over wide geographic areas causing food shortages to become widespread. These factors may combine to produce widely fluctuating populations of squirrels. These fluctuations would, in turn, impact species dependent on squirrels for prey such as goshawk and marten. Since red squirrels are specifically dependent on conifer seeds as a food source, they are impacted by timber harvest in much the same ways as are seed-eating birds. Benkman cites research that indicates that Sitka spruce does not produce seed-bearing cones until it is 20-40 years old. Douglas fir does not reach its peak potential until 200 years of age. Extensive harvest of mature trees may therefore have far-reaching effects for the vertebrate populations dependent upon their seed production.

6.14 Great Blue Heron

Many reviewers agree that the great blue heron would not serve well as a management indicator species since the Tongass National Forest represents the outer edge of its range. However, this species may still be of important management concern and the location of known rookeries within the Tongass National Forest should be mapped and those areas should not be disturbed.

6.15 Northern Goshawk

This species is likely to become protected under the Endangered Species Act. Thus, management planning with regard to the northern goshawk will need to be especially conservative. Because goshawks require large territories to thrive, several reviewers are of the opinion that even large HCAs were not

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adequate to meet its needs. Forsman also points out a number of problems with the data on which the goshawk model was based. There does not appear to be adequate data either of current or historical nature and scarcity of the birds may or may not be a function of habitat fragmentation. The goshawk serves as an example of the primary importance of immediate research with field inventories.

6.16 Boreal Owl

The plan for this species also suffers from a lack of data on which to base recommendations. Powell places the boreal owl in the same category as the great blue heron in that the Tongass National Forest represents the outer limits of its natural range so it may not be a suitable indicator species. Forsman points out that the management of the habitats, including second-growth, around HCAs will be critical in determining viability for the boreal owl as well as most other species under consideration.

6.17 Northern Flying Squirrel

The northern flying squirrel differs radically from red squirrels in its habits and the food supply on which it depends. It is quiet and nocturnal and feeds on lichens and fungi in old-growth trees. More information is needed on its relationship to predators such as marten and goshawks given the viability concerns for the latter.

6.18 Blue Grouse

Ratti makes three points about the blue grouse model: 1) the species probably does not warrant classification as a "major game species," 2) the data reported do not support the conclusion that the blue grouse are negatively affected by clear-cut harvest, 3) concerns about the estimated density of the birds based on whether or not non-breeding males are silent, or whether silent males are necessarily non-breeders.

7 Recommendations on Information Needs and the Planning Process

In this Section we will outline a program of work to provide a solid basis for a biologically defensible plan. These recommendations are for data collection and are to be built on the consideration of the multiple paradigms discussed in Section 4.

7.1 Planning and Planning Documents

Clearly the planning process must be more unified. The three documents we reviewed together with new information need to result in a single, well written, and edited document. The wildlife part of the Plan must, in turn, be much

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better integrated into other aspects that affect wildlife such as fishing, hunting, and recreation. In particular a synthesis of this work on wildlife, the work on the species proposed for listing under the Endangered Species Act, and the PACFISH effort must be undertaken. The entire plan must then be integrated to make clear a range of options and their associated trade-offs.

7.2 Challenges and Limitations to Data Collection

The sheer size of the Tongass National Forest obviously limits the amount of data that can be collected on a per acre basis. We believe, however, that collecting quality data for some species and for some environmental mapping can provide a biological gauge for the rest of the system. The MIS process is an example of this approach and we recommend adding the efforts outlined below.

It is worth reiterating that the MIS approach as well as the other approaches we recommend all suffer some limitations. The most important limitation to keep in mind is that knowledge of any one species does not automatically translate to knowledge of other species and that, consequently, management to protect one species does not automatically protect other species.

7.3 Immediate Management Recommendation: Keep Landscape Options Open

We are very concerned that during the time necessary to complete the short-term research recommendations below, options for alternative landscape design scenarios be kept open. In particular we recommend that:

1. The existing largest blocks of contiguous high volume old-growth forest not be further fragmented by timber harvesting or road building.

2. The letter and spirit of the provision against highgrading in the Tongass Timber Reform Act (TTRA Title III Sec 302 C 2) be strictly adhered to. Operationally this amounts to not differentially cutting in low altitude, high volume stands (greater than 30 thousand board feet per acre). Meeting the recommendation will require compensatory lowgrading.

These recommendations are motivated by three arguments:

1. In the absence of data and analyses much care is called for.

   We do not have a good enough account of the current fragmentation pattern on the Tongass National Forest and the effects of natural fragmentation and habitats other than old-growth have not been factored in.

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2. Decreasing options now may force more expensive choices later.

This has been a major lesson from the experience of the Forest Service in the Pacific Northwest. Also the high cost of implementation of species recovery plans under the Endangered Species Act has shown that it is much more economical to save species when they are still common.

3. Viability of certain species near or below their minimum populations will be further reduced.

Concerns have already been expressed about viability of brown bear and wolf given the HCA recommendations of the *Strategy* and anticipated harvesting levels. A redesigned landscape plan will therefore need to consider larger areas than those proposed, especially in areas of high volume old-growth. This cannot be done without maintaining larger areas. In addition the life history of martens indicates that dispersal requires wider corridors than have been proposed. The need for wider corridors means again that old-growth be available for landscape design.

7.4 Short-term Management Recommendation: Data Acquisition

We do not think it necessary that an extraordinary amount of long-term research be done to develop a biologically defensible plan. However, in the short term there is work that must be done to give a clear enough picture of wildlife and conservation on the Tongass National Forest to form the basis of a solid plan. We recommend a short-term program of 1 to 4 years with the following elements:

7.4.1 Construct a PVA for a Single Large Species.

We feel that there is currently enough information available for the Brown Bear to construct a Population Viability Analysis for that species on the Tongass National Forest in a 1 to 2 year period. This analysis should be dynamic and spatially explicit. Recalling Figure 1 we see that we have chosen a species to the right of the graph. That is, this is an animal for whom the fragmentation of the Tongass National Forest is important with regard to problems of dispersal and metapopulation maintenance. The viability of this species is currently problematic and any clarification of its status will have an important impact on future planning efforts.

7.4.2 Perform a Detailed Evolutionary/Genetic Analysis for a Single Group of Small Mammals.

Three genera of rodents are already known to have substantial evolutionary and genetic variation on the Tongass National Forest: *Microtus*, *Peromyscus*, and *Clethrionomys*. Part of the genus *Peromycus*

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has been the subject of a recent revision which included some samples from the Tongass National Forest (Hogan *et al.*, 1993). This study revealed new patterns of variation and realigned species and subspecies within the forest. The comprehensive methodology of this study should be extended to an analysis of single populations from small islands and multiple populations from large islands and the mainland with barriers between drainages. The choice of which of the three genera to analyze should be based on a preliminary screen of existing museum specimens. This analysis is selecting a species from the left side of the graph in Figure 1 and focusing on the evolutionary and genetic effects of fragmentation.

7.4.3 Construct a Three-dimensional "Photograph" of the Physical and Biological Environment of the Tongass National Forest.

Perhaps the most pressing need for the planning process is a visual three-dimensional account of the *current* physical and biological environment. Recalling the famous quote "Your hands can't hit what your eyes can't see" we believe that rational management is not possible without such a visual picture. The question is how to create it. Remote sensing is the obvious idea. But at high latitudes there are difficulties with the geometry of the satellite sensing systems and these are further confounded by the rugged topography and the frequency of cloudy days. These considerations have traditionally militated against doing remote sensing on the Tongass National Forest and there is at the moment no off-the-shelf, production method available. We believe, however, that a second look at remote sensing may find ways of getting the picture that is needed. We observe that for wildlife, as opposed to timber, remote sensing may not have to be done at the higher resolution of LANDSAT Thematic Mapper Imagery. Rather lower resolution imagery (possibly AVHRR) may provide enough of a picture of the current pattern of forest and fragmentation to make sound wildlife decisions. This imagery would then be combined with as detailed a Digital Elevation Model (DEM) of the Tongass National Forest as can be constructed. Perhaps the DEM could be supplemented by Synthetic Aperture Radar to give a higher resolution to the topography. Clearly these recommendations will require some research to implement, but some progress must be made in this direction to give the Tongass National Forest the ability to manage in three dimensions as is necessary.

7.4.4 Develop a Preliminary Understanding of the Relations between Regeneration, Second-Growth, and Wildlife.

The three documents under review all focused on the old-growth relations of the species chosen. But a complete analysis will depend on understanding how wildlife interacts with all habitats on the Tongass National Forest. Some species associated with old-growth will also be able to use second-growth generally, others will need second-growth for

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dispersal between patches, and some may never enter second-growth. For those species that use second-growth in some way, overall viability may depend on the kind, amount, and spatial distribution of second-growth that exists. For example, it is likely that marten can disperse through some kinds of second-growth, but not through very dense young stands. Also Alaback (1982) has shown that some kinds of second-growth have low populations of mammals. Those species such as the red squirrel and crossbills which require seed producing trees may also be able utilize only certain kinds of second-growth. The plan needs to contain this kind of information, especially if the HCA paradigm is the only one chosen, for then the nature of the habitats between HCAs becomes critical. Therefore, an important research need is to develop a map of the kinds and distributions of second-growth, to understand the relation of the kinds to different species viability, and finally to understand how to manage second-growth to produce the necessary kinds and distribution of second-growth. It is likely that by factoring in other habitats besides old-growth that some species will have increased estimated viability, while a knowledge of the inability of others to disperse through second-growth will decrease their estimated viability.

7.4.5 Initiate a Biological Survey of the Tongass National Forest.

One of the most frequently recurring themes in the individual reviews is that we do not now know all of the species that are on the Tongass National Forest and very little about the distribution among islands and watersheds of the species we do know are there. There is a pressing need for a thorough biological survey of the Tongass National Forest. Such a survey is not something that must be completed in the short term, but it should be initiated soon. Beyond beginning the planning process for such a survey, an important first step could be accomplished by organizing all of the museum specimen locality data that currently exists. For example, The Museum of Vertebrate Zoology at the University of California at Berkeley has hundreds of specimens from southeast Alaska. Several other museums likely have large collections as well. Compiling and mapping that data will give an important initial picture of what is known about species distributions on the Tongass National Forest and could form the basis for the statistical design of the survey.

7.5 Long-term Management Recommendation: Adaptive Ecosystem Management

While, as indicated above, ideas about ecosystem management are still in a state of flux, three principles that seems to be common to all visions of ecosystem management are that it: 1) should be adaptive, learning from experience, and changing in response to new ideas, information, and

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conditions; 2) should be based on natural patterns of disturbance; and 3) should integrate a species approach (e.g., PVA) with a landscape approach.

7.5.1 A Process for Adaptive Ecosystem Management

While the previous sections of this report provide recommendations for short-term responses to the issues raised by this review, more comprehensive and longer-term strategies must provide the basis for land management planning on the Tongass National Forest. The developing paradigm of adaptive management provides a framework within which to organize planning, on-the-ground activities, monitoring, and evaluation in an iterative process. Several of the reviewers cited the adaptive management methods outlined in the FEMAT document (FEMAT, 1993) as having the potential to organize management activity in such a way as to meet both the letter and the intent of the legislation previously cited.

The FEMAT strategy is based first on the consideration of the different topographic scales of the Tongass National Forest in terms of region, province or river basin, watershed and specific site:

Region - The current Tongass Land Management Plan was developed with an emphasis on regional scale and pattern. This emphasis constitutes some of the strength of the plan.

Province/River Basin - The island nature of Tongass National Forest topography virtually imposes consideration of the provincial scale on the planning process.

Watershed - As noted above, the dendritic character of the Tongass National Forest landscape created by extreme variations of terrain also dictates an inclusive perspective as it relates to wildlife habitat.

Site - Each site is embedded in the scales above, but also has its own characteristics. In addition, the character of the sites just adjacent to a given site are important (see Section 4.4).

An informed awareness of these measures of scale provides the geographic context within which the adaptive management process must function. Adaptive management is based on the premise of "managing to learn." It assumes the dynamic, stochastic nature of the environment by building in mechanisms for responding to change. Not only is the state of the environment and resident organisms always in flux, so is the degree and sophistication of our knowledge about them. As information becomes available, as conditions change, management strategies must have the flexibility to respond as an integral part of a feedback loop. The figure below illustrates the process and is derived from the FEMAT report.

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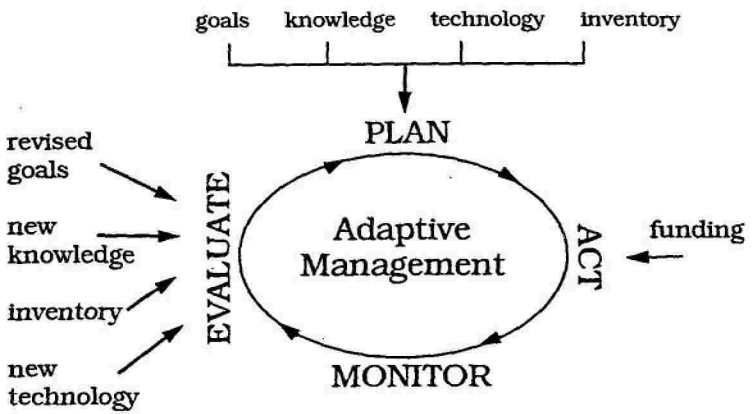

Figure 2: Process of Adaptive Management

Initially, the planning process must be based on a variety of alternatives which may each be tested in appropriate locales. The Habitat Conservation Areas may be specifically appropriate for the larger islands of the Tongass National Forest and could be implemented based on some of the criteria outlined in the existing land management plan provided some of the details are modified to address specific concerns outlined in this report. Large islands may also serve as sites for developing innovative timber harvest methods that are more consistent with the natural, long-term forest cycle dynamics. Because wildlife on the smaller islands has less opportunity for dispersal and is therefore more vulnerable, these areas may be candidates for experimental forests and/or exclusive reserves within which timber harvest would not be permitted. Early planning efforts must incorporate specific research mechanisms for monitoring the effects of each strategy. Scientific research and outcome evaluation must inform management decisions during each phase of the adaptive process. This implies an integration of the efforts of a variety of agencies and interests in the cooperative spirit of the interagency committee that developed the *Strategy* document. In addition, the monitoring process provides an opportunity to invite the participation of research institutions to gather data to further knowledge of the ecosystem as well as to support decision-making activities. Several of the reviewers of the Tongass Land Management Planning documents expressed concern about the lack of needed data on

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which to base appropriate management decisions. The adaptive management process also requires relevant data from in-depth inventories of biological, economic, physiographic, and human social characteristics of the region. The very breadth of the task implies a broad base of interested inquiry into the factors that determine the future of the area.

Beyond these broad topics, the FEMAT document also outlines several standards that would establish quality control criteria for the development of this complex information base. (FEMAT, 1993, VIII-26).

- Boundary neutral - should cross administrative and ownership boundaries.
- Multiscale outputs - useful at all scales.
- Dynamic - includes and monitors trends.
- Social, economic, biological, physical components.
- Geographic information systems and remote sensing capability.
- Quality control standards and processes.
- Cost efficient.

Because the Tongass National Forest represents some of the biologically richest boreal old-growth forest lands remaining in the world, it provides a window of opportunity to implement new management strategies that may not only meet the letter and intent of federal law but may also avoid foreclosing biological and economic options for the future.

In summary, the concept of adaptive ecosystem management implies that options are to be kept open. In this context we conclude that ***a long-term timber contract is the logical antithesis of adaptive ecosystem management***.

7.5.2 Manage on the Basis of Natural Disturbance Regimes

This is a common theme in most ecosystem management discussions. Natural disturbance regimes on the Tongass National Forest are little known. We do know that this forest is only about 10 thousand years old and any analysis of natural disturbance would begin at this time scale and work down to shorter intervals. We do know that patterns of natural disturbance are specific to particular soil types (Bormann and Sidle, 1990) so soil considerations may play a greater role in determining management practices than heretofore.

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7.5.3 Synthesize Species-based and Landscape-based Approaches

We have already discussed this idea in Section 5.6. Here we will simply reiterate that this is a vision for the future that provides direction for what must begin now.

7.6 Monitoring

The scale of the monitoring task facing the Tongass National Forest is that of the plan itself: enormous. The reviews make several detailed recommendations for particular species, but overall we have concluded that, since there are so many issues surrounding monitoring, a separate monitoring plan should be produced and an outside review of it obtained. The biological survey research initiated under the Research Section above will provide much needed insight into monitoring design.

7.7 Interagency and International Cooperation

We are very enthusiastic about the development of an inter-agency approach as was begun in the *Strategy*. We hope that this cooperative style of doing business can continue and develop. To expand on this idea we strongly recommend that mechanisms for international cooperation be developed as well. For the large mammals such as the brown bear and the wolf it may be more realistic to analyze their viability over a larger region that would include British Columbia.

8 The Next Steps

The individual reviews and this synthesis are the first steps in a process of building on existing work to improve wildlife planning on the Tongass National Forest. The next step should be for the writers of the three documents to read and develop a preliminary response to these reviews. We and the individual reviewers are ready to meet and work with the authors and other planners on the Tongass National Forest. We hope that out of this process we will be able to contribute as much as possible to the planning process and to the wildlife of the Tongass National Forest.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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1. Background

Some important works guiding my review are Levins' (1969, 1970; and other authors) papers on metapopulations, Pulliam's (1988) work on source and sinks, and studies on Pacific Northwest forests (much of it summarized in Norse 1990). The first two emphasize spatial aspects of population dynamics and the last provides natural history relevant to southeast Alaska. Another critical piece of information is that old-growth Sitka spruce-western hemlock forests are largely gone from Oregon and Washington, and nearly all these forests in British Columbia are slated for logging (Beebe, 1991). Thus, in 20 years southeast Alaska may be the only area left that will contain much old-growth spruce-hemlock. Consequently, the management decisions in the Tongass will have a tremendous impact on species that require mature Sitka spruce-western hemlock forests and have large home ranges.

2. Comprehensive Review

The analyses in *Appendix M* are simple, conservative and persuasive. All logging plans discussed will imperil at least several of the species of concern, given that the proposed conservation strategy is adequate. The question is whether the proposed conservation strategy will insure species viability for the Tongass for any extended period of time.

The proposal of HCAs of three sizes somewhat uniformly scattered across the landscape seems like a reasonable strategy for protecting various populations of animals. Its success in maintaining well-dispersed populations, however, is dependent on there being sufficient movement of individuals between HCAs. This is necessary to prevent local populations from declining to extinction. This requires not only that some populations produce a surplus of individuals, but also that these dispersing individuals can cover the distances required to find suitable habitats. Furthermore, the colonization rates need to exceed the extinction rates of local populations or else the species or metapopulation will go

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extinct (Levins, 1969, 1970). Both colonization rates and extinction rates are unknown for these species in relation to the proposed strategy.

Extinction rates without repeated immigration will probably be high even in the large HCAs. Five female brown bears, 25 reproductive units of martens, and eight pairs of goshawks are not much. And these estimates are generous, especially considering that a substantial number of large and medium HCAs have already been impacted (Fig M-3 in *Appendix M*). Immigration rates, therefore, need to be high to prevent extinction. Once the forested matrix surrounding the HCAs is mostly logged off, I doubt there will be sufficient movement between populations to prevent extinction.

The "models" employ dispersal distances to recommend distances between HCAs to ensure colonization or to rescue declining populations. I am concerned that the dispersal distances used in the analyses consistently overestimate the likely dispersal distances in the Tongass. Dispersal distances reported for individuals in more continuous habitat are not likely to be the same as that found in the Tongass as it becomes increasingly fragmented. For terrestrial mammals the median (successful) dispersal distance is likely to be reduced as the habitat matrix becomes less favorable (clear-cut). Evidence for martens suggests they do not cross clear-cuts. Moreover, 20 air miles between nearest large HCAs may represent many more miles of travel by terrestrial mammals. One look at the map provided in the back of *Strategy* confirms this. In addition, only of limited number of the many possible routes lead between large HCAs, so that the success of dispersers is likely to be small. On the other hand, for birds, such as the goshawk, dispersal distance might increase with increased fragmentation.

Colonization rates depend also on the rate of production of surplus individuals. The production of surplus individuals will surely decline as high volume, low-elevation forests are logged and total forested area declines. The proposed HCAs will be even less able to maintain viable populations than estimated.

In the absence of the above information I would suggest a strategy incorporating the "20 pair rule" (Thomas *et al.*, 1990) and providing corridors of mature forest between HCAs, as recommended by the study on flying squirrels.

Particulars of *Strategy*

p. 31. (3) Why is salvaging permitted within HCAs? Work from the Pacific Northwest shows how important downed and dead trees are to ecosystem function. Moreover, burrows under snags provide important dens to river otters (p. 231 of *Strategy*). Snags are important to flying squirrels too (p. 254 of *Strategy*).

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p. 34 (5) It is said that the "best management practices would be 600 ft" buffers, yet a minimum of 300 ft is recommended. Why? This is also done on p. 35 (6).

p. 35. River Otter. What is the width of the riparian old-growth buffers? 1,000 ft? 300 ft?

p. 37. It is unclear why small watersheds were ignored in the location of small HCAs. Although the habitat may be limited, it does not mean the habitat is not important as a corridor. In fact, if habitat is limited in the first place, small areas may be even more critical as dispersal corridors.

3. Species Review

Appendix B. Species Accounts and Individual Conservation Strategies

Queen Charlotte Goshawk: This subspecies is endangered based on the information given by the author. For example, he says that "the remaining total international population of Queen Charlotte goshawks is similar in size to that thought minimally viable" (p. 132). Thus, the conservation strategy needs to be very effective in protecting the remaining goshawks. Yet, the recommended HCA sizes and distances between them inadequately protect the goshawk. Large HCAs need to support eight pairs of goshawks, but based on the authors earlier work large HCAs will support at most three pairs of goshawks. Similarly, medium HCAs will usually support no goshawk pairs, not two pairs.

Boreal Owl: I agree with the boreal owl recommendations. In particular, more information on their occurrence and distribution is critical. Some higher elevation old-growth forests in southeast Alaska might be relatively good habitat for the boreal owl. I would think that elevational transects would be helpful. Maybe most of the boreal owls occur at higher elevations and are in good shape.

Marten: The distance of 40 km (25 mi) between large HCAs was chosen because it is near the maximum dispersal distance recorded for martens. This distance might be all right if medium and small HCAs served to connect large HCAs. However, this seems unlikely considering the dispersion of large and medium HCAs as in the map at the back of *Strategy*. In addition, small HCAs are unlikely to serve much of a function for martens (only enough area for one reproductive unit). Moreover, martens apparently avoid crossing clear-cuts.

Mountain Goats: It recommends sufficient habitat that can support at least 50 goats be maintained based on Berger's (1990) study of mountain sheep. This might be all right if there is movement between populations, but if they are

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isolated (and assuming the sheep work can be extended to goats) 100 goats per HCA would be necessary (see Berger, 1990).

Models

The habitat capability models seem like a reasonable method to get an idea of the general impact on different species of altering habitat. The models will surely vary in their usefulness depending on the amount of biology incorporated. I did not read these models that closely. However, glancing at the red squirrel model, I think from the text that habitat value of young stands of spruce/hemlock is likely to be overestimated. On p. 5 of this model it is mentioned that "Heavy cone and seed production has been reported in 100 year-old stands of western hemlock and Sitka spruce indicating valuable habitat for red squirrels (Ruth and Berntsen, 1955)." It should be noted, however, that only 4% of the seed produced was spruce seed; the rest was hemlock seed. Hemlock cones are much less valuable to red squirrels than are the much larger spruce cones.

4. Comprehensive Recommendations for the Future

4.1 Philosophical and Conceptual Considerations

A major concern is the effect that logging (e.g., Plan P) will have on species is not considered by the conservation strategy. In particular, there is a recently described species of crossbill (Groth, 1993) that appears to be adapted to Sitka spruce (Benkman, 1993a, unpublished data). Crossbills are a speciose lineage. What had previously been recognized as a single species, the Red Crossbill (*Loxia curvirostra*) in North America, consists of at least seven distinct species (Groth, 1988, 1993). Moreover, most if not all these species of crossbills are adapted specifically for foraging on single species of conifers, and sometimes just one variety of conifer (Benkman, 1989, 1993a, unpublished data).

Two species of red crossbill occur in the Sitka spruce-western hemlock forests of southeast Alaska. One is adapted specifically for foraging on seeds in western hemlock cones, and the other may be adapted for foraging on Sitka spruce (Benkman, 1993a). The western hemlock crossbill is common in areas of good cone production, but the Sitka spruce crossbill is rare even in the best habitats (Benkman, pers. obs.). Based on my knowledge of this crossbill and other crossbills (Benkman, 1987, 1988, 1989, 1990, 1992, 1993a, 1993b), the Sitka spruce crossbill received a total score of 123 in terms of the evaluation criteria used for the other species of concern. This is the fourth highest score, and places it between the mountain goat and gray wolf in the level of concern. This is very much greater than the 20 "red crossbills" received in Table 4C of Appendix C in *Strategy*.

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The relative rarity of the Sitka spruce crossbill can be attributed, in part, to Sitka spruce being less common and producing seeds less regularly than western hemlock. Its rarity, however, makes it more vulnerable to any process that reduces the abundance of cone producing spruce trees and increases the likelihood of cone failure. Logging has the potential to greatly reduce seed production, and, in turn, reduce the abundance of conifer seed-eating birds (Benkman, 1993b). For example, logging increases the domination of forests by younger trees (Harris, 1984), which produce smaller and fewer cone crops than mature forests. Sitka spruce does not produce cones until it is 20-40 years of age (Fowells, 1965), and like most conifers it only produces large cone crops when it is older (see Burns and Honkala, 1990). For example, Douglas-fir does not begin maximum cone production until it reaches 200 years of age (Fowells, 1965).

Lower densities of conifer seed-eating birds (Pine Siskins, Red Crossbills and White-winged Crossbills) have been found in young second-growth than in old-growth habitat (Manuwal and Huff, 1987; Huff *et al.*, 1991; see also Raphael *et al.*, 1988). In addition, logging appears responsible for the tremendous decline of Red Crossbills in northern Finland (Vaisanen *et al.*, 1986; see also Helle and Jarvinen, 1986).

Crossbills require large areas of mature forests throughout their range (Benkman, 1993b). This is because in any given year large conifer cone crops are usually produced in only a limited area. This is where crossbills concentrate. Thus, many different regions may be essential for the survival of the crossbill over a five or ten or more year period. Consequently, a severe reduction in any one area will disproportionately affect the crossbill population because in any given year most if not all of the population might rely on the cone production in that region. Extensive logging in the southern Tongass (let alone the even more extensive logging south of Alaska) will be very detrimental to crossbills.

What I find potentially troublesome about the proposed management plans is the effect on the percent of the productive old-growth remaining in each of the ecological provinces. By 2110, many ecological provinces will have only about 75% of their productive old-growth left. By 2140, most provinces will have less than 75% left. Is 75% enough? It is difficult to know and requires study. However, an analysis of the Annual Christmas Bird counts suggests that 75% may not be enough. Six counts in southeast Alaska have been conducted five or more times (range 5 to 18 counts, mean = 12 counts). Five counts occur in ecological provinces where about 90% or more of the 1954 productive old-growth remains (estimated from Fig. M-3 in *Appendix M*). Red crossbills have been observed on these counts an average of 0.38 of the years (range of means for the 5 counts: .20 to .61). One count (Craig) occurs in an ecological province where only about 75% of the 1954 productive old-growth remains. On none of the nine counts (going back to 1981) have red crossbills been recorded. Red Crossbills were common in at least one winter in this area in the early 1900s (Willett, 1921).

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In several places (e.g., p. 132 of *Strategy*) longer rotations were mentioned as possible management considerations. Longer rotations seem to be necessary for the conservation of many species. With longer rotations (e.g., 200-300 or more years) in mind, the rate of logging in areas outside HCAs and Wilderness Areas needs to be reduced so that current logging rates are sustainable over the next 200 to 300 years.

4.2 Program of Research

Most of the proposed research seems valuable. In addition, we need data on dispersal in habitat that is in a matrix of clear-cuts and young second-growth. We also need to know extinction rates as patch size decreases and isolation increases.

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Tongass National Forest
Land Management Plan

Scientific Review

by

Eric Forsman
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USDA Forest Service

(Note: Dr. Forsman's comments pertain only to the *Strategy* sections for the boreal owl and goshawk. His comments are keyed to specific references in the document text. Locations are specified at the beginning of each comment where applicable.)

1. Background

I very quickly read through the introductory section (pp. 7-43) and did not have any major problems with that section. I may be somewhat biased, but in general I think the meta-population approach proposed in the introduction is a reasonable compromise given the needs of humans and the considerable uncertainty that we always seem to have regarding the persistence of wildlife populations under different management scenarios.

A couple of general comments that apply to both species are summarized at the end of my comments. Basically, these summary comments point out the obvious - that it is difficult to develop a bullet-proof management plan when you have little data and what appear to be sparse populations. I also strongly emphasize the need to get on with an accelerated program of monitoring and research to document the kind of information needed to do a good management plan.

2. Species Review

Boreal Owl

(Page 140, last paragraph) I think this is too strong a statement - there is no evidence to indicate that this species occurs throughout the mountains of Oregon and Washington. We have never heard them in the Coastal Mountains of

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either state. I am also unaware of any records of breeding in the Cascades of Oregon. I think you should be a bit more cautious here.

(Page 140, first paragraph) Are these findings from Europe? If so you might point out that habitat use could differ some when you are on another continent.

(Page 142) I am not very familiar with this literature, but am a bit suspicious that anyone has been able to do a very thorough job of quantitatively assessing prey abundance within different home ranges, and then doing a statistical comparison of owl productivity relative to prey abundance. That sort of study would require a large number of radio-marked pairs, as well as detailed knowledge of seasonal prey abundance within the home range of each pair. I would also want to know the age of the birds, since age can have a lot to do with productivity. My suspicion is that these results are based on samples of a few pairs and a whole lot of conjecture regarding the relationships involved rather than detailed statistical comparisons. If I am wrong, then disregard this paragraph.

(Page 144) I don't think you can say this about SE Alaska. At this point you really don't have any data to show that the presence of nest sites is a limiting factor in that area. You may suspect it is the case, but you have no data on the availability of nest cavities from what I can tell. Be very careful to make it clear when you are talking about facts and when you are talking about hypotheses.

(Page 147) In the absence of much data on the abundance of the species, this management approach should definitely be viewed as a very short-term solution. Unless you have about 15-20 pairs of owls in each of your conservation areas, there is reason to believe that they may not be large enough to sustain a viable metapopulation over the long haul. As it stands right now, you just don't appear to have the kind of data that one would need to assess the adequacy of the reserve network relative to boreal owls. The adequacy of this approach is also going to have a lot to do with the kind of matrix in which the reserves are located. Would the matrix largely be a free-fire zone in which intensive timber harvest was largely the order of the day (except for areas around known nests)?

I definitely agree that you badly need to implement a monitoring plan to find out what you have to manage!

Queen Charlotte Goshawk

(Page 101, last paragraph) In my experience, these kinds of models are only as good as the data that goes in to them. In the case of the goshawk in SE Alaska, it appears to me that you have next to no data on historical or current population levels. Based on the preliminary data from the telemetry study in SE Alaska, it also appears to me that you may be totally underestimating the amount of

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habitat and area being used by Goshawks in your model. After reading your report I am left with one dominant conclusion - all we can say about goshawks in SE Alaska at this point is that they are relatively rare, and that they are probably declining as a result of habitat loss. Going much beyond that is pretty much a guessing game. What you have is considerable evidence that suggests that goshawks are not particularly plentiful in SE Alaska. Given the lack of quantitative data, I do not find it at all surprising that there is a lot of debate about the numbers.

(Page 104, last paragraph) I am not familiar with this study, but I find it difficult to believe that there is anyplace in Connecticut that is more than 600 meters from some type of significant forest opening, much less 6 miles! Is this for real? Did he get this result by requiring that clearings had to be very large, or are we talking about small clear-cut sized (20-40 acres) openings?

(Page 139, Table 1) For a variety of reasons I think Table 1 is misleading and of little value. To begin with I think the table is misleading in that it implies that goshawk densities in northwestern Oregon (zero) are somehow a function of the amount of timber harvest that has occurred there. The fact is that there is no evidence to indicate that goshawks <u>ever</u> nested in the northwest coastal mountains of Oregon north of about Roseburg. There are no historical records of breeding in that area even before the area was extensively harvested. Therefore, I think you are misleading the reader by implying that goshawk densities in that area may be a result of harvest when you have no data to indicate that they ever occurred there in the first place.

My other main problem with Table 1 is that it represents a hodgepodge of numbers from many different areas that have little in common regarding forest types or prey types that are available to goshawks. Given this situation I would expect that densities of goshawks would differ considerably among areas, regardless of levels of cutting. Thus, I think any comparisons of densities in widely different geographic regions would be greatly confounded and would be of little value in assessing the relative impact of forest removal. To put it mildly, I think this table is a real disservice to the goshawk and to science.

(Page 108, middle paragraph) I assume that your assessment is basically a guess based on the rate of habitat loss, since there is precious little data on population size either current or historical. If this is all you have to work with then that is ok, but don't beat around the bush. Very low numbers of animals is good reason to adopt a cautious approach to management.

(Page 109, middle paragraph) Could this reflect survey effort to some extent? Are areas in the south more accessible or more thoroughly surveyed? Or is there just a lot more habitat in the south?

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(Page 109, bottom) That may be their professional opinion, but I have seen no published landscape level studies that show significant relationships between goshawk productivity or numbers and measures of fragmentation in either Washington or Oregon. I think you need to be really careful regarding comments about effects of fragmentation - this is a very complex issue.

(Page 110, second paragraph) Perhaps, but this is conjecture. The fact is that there is no evidence to indicate that goshawks ever nested in the Coastal area of northwestern Oregon.

(Page 111, second paragraph) I think you mean that four of 16 territorial females did not have mates? Obviously they couldn't have been "nesting".

(Page 111, last paragraph) Where are these differences significantly different? Without statistical test results I can't tell if your conclusions are valid.

(Page 111, bottom) This paragraph is confusing to me. I also am a bit reluctant to buy the idea of a 50% or greater population decline on the Kaibab between 1972-87. In a recent discussion with Reynolds he told me that he and his crews had something like 60 marked pairs on the Kaibab in 1993. According to your assessment this would mean that the 1972 population on the Kaibab was probably in excess of 120 pairs? This seems like an awfully large population for such a small area. Does this seem reasonable?

(Page 114, first paragraph) Doesn't the Buzzard (*Buteo buteo*) count as a European counterpart of the Red-Tail? It certainly is not nearly as aggressive in taking large prey as the Red-Tail, but does to a large extent fill a very similar role.

(Page 114, last paragraph) I believe this statement is way too strong. Do you really believe that goshawks will not shift breeding locations if they lose a mate and that mate goes unreplaced for more than a year or so? They are extremely mobile animals, and I would be amazed if they did not adjust to such situations by going in search of a more suitable site, even if it only involved shifting to an adjacent territory. Unless you have really good data to support this statement, I would suggest you soften the wording a bit.

(Page 114, bottom line) Poorly worded. Sounds like they all go 60 miles exactly. I think what you mean is that most confine their movements to within 60 miles or less of the territory center?

(Page 115, first paragraph) Not to fault such experts as Brown and Amadon and Johnsgard, but I seriously doubt this. I suspect that goshawks are much like most other territorial raptors. They become very attached to a particular territory, which they defend against other goshawks. The male drives out other males, and the female drives out other females. As long as both members of the pair can exclude other members of their sex, the pair remains intact. If one or the

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other dies or is driven from the home range by another bird, the remaining bird will usually pair with whichever bird takes the place of its previous mate. Thus, I believe that the attachment is primarily to a territory rather than to a particular individual mate. As far as I can tell, the belief that raptors are "pair-bonded until one dies" has rarely been proven as a general rule, and is more fiction than fact.

(Page 115, first paragraph, last line) For the reasons outlined above, I do not buy this statement. I think it is largely conjecture.

(Page 115, last paragraph) I think this is not a supportable statement. I could just as easily argue that the fact that 44% of all juveniles in Sweden dispersed more than 30 miles is good reason to believe that gene flow would not be a particular problem with goshawks, even in widely-spaced meta-populations.

(Page 117, bottom) Yes, but there is little agreement among geneticists about exactly what constitutes a minimum viable population size.

(Page 118, first paragraph) Yes, it could be the case, but we don't know. Too much conjecture with no supporting data.

(Page 119, first paragraph) This should not be stated as a fact. It is a hypothesis.

(page 119, middle paragraph) Without some hard data, this all comes across as conjecture on your part. You may be right, but at this point it is difficult to know what is going on. What we do know is that the forests are getting cut.

(Page 121, bottom) Actually, they found that a minimum of 15 pairs was needed. However, they assumed that a certain number of sites would be unoccupied at any one time, and that to insure the presence of at least 15 pairs, the management target should be 20 suitable pair sites within each conservation area.

Comment about the General Strategy

It appears to me that you have a couple of really serious problems with developing a plan for this species. First, your survey data, albeit limited, suggests a relatively limited population, and lots of site turnover. That is, even if they are not harvested, many sites are unoccupied at any one time.

Second, the recent telemetry data collected by ADF&G suggests that goshawks on the Tongass may utilize home ranges and amounts of habitat that are much larger than in other parts of the range. If the data from the Sarkar Lake pair are representative, then it is likely that the conservation areas you propose may contain fewer pairs than the 15-20 pair target.

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In light of the uncertainty regarding population size, spacing of pairs, overlap of territories, and site tenacity in SE Alaska, I don't think you have much choice but to adopt a fairly conservative approach to managing the species, while proceeding as rapidly as possible to collect better data on the distribution and abundance of the species. Although it is not without risk, I think your proposed network of conservation areas is a reasonable start in combination with protection of known nest areas within the matrix. Without more data, I don't know what more you could do at this point, short of shutting down all harvest. Even that would not be without risk to the goshawk, since you appear to be dealing with a small, relatively isolated population at the edge of the range.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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1. Background

The US Forest Service is at the center of a revolution in natural resource management in the United States. The public is demanding increasing levels of all natural resources, from commodities to the maintenance of biodiversity. In some areas, traditional approaches to multiple-use management have not been sustaining either commodities nor ecological values (Jensen and Bourgeron, 1993; Lansky, 1992). And the courts are now holding the Forest Service accountable to a myriad of laws, resulting in economic gridlock in some parts of the country. This situation is causing the Forest Service to reassess its basic mission and operation, including: its rationale for land management, its organizational and funding structure, and the roles of science and the public in land management (FEMAT, 1993; Jensen and Bourgeron, 1993). While these events are proceeding more rapidly in some regions of the country than others, it is clear that no National Forest can avoid major transformations.

The Tongass National Forest (TNF) has features that set it apart from other national forests, including vast tracts of pristine forest, a thriving community of "wilderness" fish and wildlife species, a history of long-term timber contracts specifically designed to support local economies. Even so, the TNF will likely be held to standards for fish, wildlife, and ecosystem management that have been set in Region 6 (the Pacific Northwest) over the last five years (Thomas *et al.*, 1990; Johnson *et al.*, 1991; FEMAT, 1993). These standards depart substantially from those of the past and may require new approaches on the TNF. This review of TNF wildlife planning aims to highlight strengths of the TNF effort and recommend ways to improve the effort.

Some of the "philosophical underpinnings" to this review are as follows:

1. Managers and scientists currently do not know how to meet the mission laid out by President Clinton at the timber summit in Portland of sustaining both human and ecological communities. Our management actions should reflect the

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high level of uncertainty we have about the effects of different management approaches (Walters, 1986; Franklin, 1992; Murphy and Noon, 1991).

2. The "adaptive management" approach (Walters, 1986; FEMAT, 1993; Everett *et al.*, 1993) shows considerable promise for natural resource management. The core of the concept is to learn through management action and iteratively improve the effectiveness of management. Managers and scientists collaborate in defining management objectives, developing and evaluating alternative management strategies, implementing promising strategies, and reevaluating objectives and approaches.

3. Sustaining viable animal populations will require an expanded view of habitat that considers the potential influence of a range of driving factors, (e.g., vegetation, climate, geomorphology, human activities) on animal populations at different spatial and temporal scales (Hansen *et al.*, 1993; Turner *et al.*, 1993). Maintaining viability for some species will require detailed studies of both habitat patterns and population demography.

4. New, more cost effective approaches need be developed to meet the requirements of the National Forest Management Act involving: inventorying, monitoring, and projecting the past, current, and likely future status of animal habitats and populations (FEMAT, 1993).

5. Environmental decision-making can be improved through analyses that better integrate and quantify the interactions of ecological, economic, and social factors (Constanza *et al.*, 1993).

2. Comprehensive Review

Document 1: *A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska*

General Approach

The core approach of this report is scientifically sound and generally consistent with modern conservation biology. The Interagency Committee was somewhat "trend-setting" in starting with a list of all terrestrial vertebrates and then using objective criteria to identify the species with the highest risk of becoming inviable. This "multispecies" approach was advocated by as an key step for managing vertebrate communities by Hansen *et al.* (1993). The approach was also put in practice by the USFS in Region 6 under court order (FEMAT, 1993).

The committee's conservation strategy for those species considered at risk is fashioned after the approach used for the Northern Spotted Owl (Thomas *et al.*,

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1990; Murphy and Noon, 1992). The spotted owl plan drew heavily on island biogeography and metapopulation dynamics theory, and has generally been supported among ecologists and conservation biologists. Both the spotted owl plan and the Tongass strategy emphasize a network of reserves, each of which is large enough to support breeding populations. Immigration and emigration among the reserves is facilitated by optimizing the distance between reserves, by maintaining habitat patches for dispersing individuals, and by maintaining forested corridors among the reserves. I believe this regional approach is especially appropriate for the TNF because this forest supports several species that use habitats over large spatial scales and are likely vulnerable to cumulative human impacts, and because many forest patches in the TNF are isolated by waterways and mountains which may constrain dispersal opportunities. The committee appears to have done a good job at establishing criteria for the reserve network and in mapping out an implementation of the network. Overall, the committee makes a good case that this design is a minimum needed to meet the population viability requirements of the National Forest Management Act.

The interagency strategy does have some shortcomings, however, that should be addressed.

1. By focusing exclusively on species associated with old-growth spruce/hemlock forests, other species that are at risk may be overlooked. The TNF contains other vegetation types (e.g., muskeg, salt-spray zones, shore pine forest, deciduous-tree dominated flood plains and avalanche zones) that may support species at risk. Road building, logging camps, recreation, firewood cutting, and other human activities may occur in these habitats and influence any sensitive species residing there.

Species found in early-seral forest habitats should also be evaluated. It is possible that such species have historically been rare in the Tongass because of infrequent canopy-replacement disturbances and that these species do not find clear-cuts as suitable habitats.

2. A similar effort should be done for aquatic species, especially fish. It is extremely important to determine if any species or spawning runs are at risk or (likely to become at risk) and to develop management strategies for these species.

3. The plan gives too little consideration to maintaining ecosystem types and ecosystem processes across the forest. FEMAT (1993, pgs II-101 to II-103) reviews the strengths and weaknesses of "species-based" verses "ecosystem-based" conservation strategies and concludes that both approaches are needed to meet the National Forest Management Act. Maintaining the full array of ecosystem types and processes helps to ensure that the organisms associated with these ecosystems and processes will be maintained.

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4. The plan does not draw sufficiently on studies of disturbance, forest succession, and landscape dynamics in presettlement times. Many ecologists suggest that knowledge of presettlement pattern and process provides a context for current and future land management (Swanson *et al.*, 1993). For example, I wonder how stand and landscape patterns generated by clear-cutting on the Tongass compare with those created by natural disturbance. My guess is that there are few other national forests in the country where current silvicultural practices differ so much from natural disturbance as on the Tongass. The Northern Rockies Region, in contrast, strives to maintain landscape patterns that are within the range of variation of presettlement times.

Knowledge of presettlement disturbance and vegetation dynamics seems especially important in the Tongass. It appears that vegetation in southeast Alaska is still responding to climatic conditions of the Holocene and the Little Ice Age (ca. 300 years ago). Some forests there are the first to invade deglaciated or nonforested habitats. Also, alpine tree line continues to increase in elevation. Would we expect "first-generation" forest ecosystems to be as resilient to logging and other disturbance as forests that have been in a dynamic steady-state for several generations? Are there implications here for the placement of HCAs? Similarly, I wonder if gap phase dynamics differ much between the sites on wind-swept slopes with shallow soils and relatively wind-free sites with deep soils? Does habitat suitability for wildlife differ between these two forest types? Can old-growth be maintained in HCAs that are placed in disturbance-prone areas?

5. The strategy also does not deal much with environmental gradients across the Tongass that may strongly influence vegetation dynamics, wildlife habitat suitability, and animal species diversity. Factors such as latitude, elevation, slope position, soil type, hydrology, and climate are know to influence vegetation dynamics and wildlife diversity. Given that these factors vary dramatically across the Tongass, they should be considered in designing a conservation strategy.

6. The conservation plan tends to ignore the matrix of forest lands outside of the specified forest reserves and corridors. There are perhaps two shortcomings to this. First, it assumes that activities in the matrix will not reduce the quality of habitat within the reserves and corridors. What is the likelihood that clear-cutting adjacent to corridors or HCAs will result in substantial blowdown within those corridors or HCAs? Second, it assumes that corridors will be sufficient to allow animals to disperse among HCAs. The current spotted owl plan, in contrast, specifies managing the matrix to maintain a certain level of canopy cover to allow owl dispersal.

7. The plan would be of more use to decision-makers if it laid out a range of alternative designs (rather than just one) and analyzed the ecological, social, and economic trade-offs of each (e.g., Johnson *et al.*, 1991).

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Specific Methods

1. The initial screening of species should include all species of vertebrates, not just those associated with terrestrial habitats or with old-growth. This will ensure that sensitive species using other habitats will not be overlooked.

2. Consider adding to list of Evaluation Criteria (pg 14-20) the current and likely future area of suitable habitat for the species. Area of suitable habitat has been found to be a good predictor of population size. GIS analyses and simulation models are required for this analysis, but these tools are available and should be used on the Tongass (e.g., Hansen *et al.*, 1993).

3. Stratifying the conservation plan by ecological province seems an attractive approach for both tailoring the plan to more local conditions and maintaining well-distributed habitats.

4. The main factors used to determine reserve boundaries were seral stage, above ground biomass, patch size, and distance from other reserves. Other factors that may merit consideration include: proximity to streams and/or coast, slope position, elevation, soil type, natural disturbance regime, and climate. For example, a 40,000 acre HCA that is predominately in uplands would provide a much smaller area of suitable habitat for a species requiring flood plains. Also, an HCA in an area prone to natural disturbance may have less longevity for old-growth species than one with a mild natural disturbance regime.

5. Retaining travel corridors along the coast and in riparian areas makes good sense. Should the matrix also be managed so as to both protect the travel corridors and to allow some level of dispersal through the matrix?

6. The additional standards for species of concern (pgs 31-36) seem well formulated and appropriate.

7. In provinces where the HCA criteria could not be met, should silvicultural strategies be used to restore suitable habitats?

8. The viability/distribution risk assessment is a good example using the conservation strategy as a benchmark for comparing other management alternatives (in this case, forest plan alternative P).

Quality of Information

A persistent problem with conservation planning is that most species are little studied and poorly understood. Two approaches are generally taken in this case. One uses the best available information on sensitive species (poor as that

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may be) to design the conservation plan. The hope is that a plan that works for the better known species will also be suitable for lesser known species. The second approach is to maintain the full range of natural ecosystem types and natural ecosystem processes. The idea here is that native species are adapted to these ecosystems and processes and will persist if the ecosystems and processes persist.

The committee used the first approach. I think they did a good job of synthesizing the available information. I suggest, however, that an effort like this should be complemented with one that focuses on ecosystems and processes.

Whichever of the two approaches is used, it is essential that research and monitoring be used in the long term to fill important knowledge shortfalls. Adaptive management offers a construct for gathering this information. I believe that the Tongass (and the Forest Service in general) will have to put substantially more personnel and funds into administrative studies, research, inventory, and monitoring in order to meet the viability regulations in the National Forest Management Act. It is likely to be more cost effective to fund such information-gathering efforts now than to be forced by ignorance to implement overly restrictive conservation plans.

Document 2: *Appendix M. Fish and Wildlife: A Viability Risk Assessment*

General Approach

The "Species Review" section of this document is very confusing and hints at major problems in the forest plan. First it says that standards and guidelines were written for endangered, threatened, candidate, and sensitive species, and that consequently, there is no need to analyze their viability in this document. Later it says that these standards and guidelines are too weak to prevent species from becoming viability concerns. Similarly, the document says that the management indicator species (MIS) have been thoroughly modeled for each of the management alternatives, but that the models are too poor for province-based assessments of risk to viability. All of this suggests that neither the standards and guidelines nor the MIS analyses and models are sufficient for assessing current or future viability concerns.

The "Analysis of Wildlife Population Viability" (starting on pg. m-10) is valuable in comparing past, current, and possible future old-growth abundance under each of the management alternatives. The "pinch-point" analysis and the analysis of effects of cutting on the proposed HCAs is also useful in giving consideration to the spatial patterning of the remaining old-growth.

The major weakness is in drawing inferences about wildlife population viability based on patterns of old-growth. This analysis of old-growth clearly

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needs to be supplemented with a species-based approach. It would seem a merging of this effort, the Interagency effort, and the habitat capability modeling effort is needed to best understand the likely effects of the management alternatives on species viability.

Specific Methods

1. It is not clear why so few of the species designated as "sensitive" by the Regional Forester were scored as "at risk" by the Interagency Committee. This suggests a conflict between the criteria used in the two analyses.

2. The Management Indicator Species (MIS) Approach, as described in this document, does relatively little for maintaining species viability. Few of the criteria listed on pgs M-7&8 deal with viability. The criteria also do not seem to be well designed to identify species that are likely to be representative of several other species in their response to habitat change. So it is not clear to me what the purpose of the MIS approach is.

The notion that a few species are good indicators of habitat needs of many other species is on shaky conceptual grounds (Landres *et al.*, 1988). Moreover, it is seldom implemented in ways to ensure likelihood of success. I personally advocate the approach taken by the Interagency Committee where objective criteria relative to viability are used to evaluate all species. Those most at risk can then receive a disproportionate share of the research and conservation effort (see Hansen *et al.*, 1993).

3. Why were endangered, threatened, candidate, and sensitive species excluded from the risk assessment? It seems insufficient to say that standards and guidelines for these species are in the forest plan, so risk analyses are not needed. MIS were treated more rigorously. Habitat capability models were developed and used to assess the various forest alternatives. Why was this done only for MIS species?

4. The summary on pg M-10 is very confusing. The document identifies several groups of animals for which there is concern over viability (this is how the sensitive species were defined). Paragraph 2 in this section then says that there are "no current viability concerns" and suggests that the forest standards and guidelines are too weak to prevent species from becoming viability concerns. This bit of doublespeak indicates that the forest plan does not offer sufficient protection to prevent species from becoming inviable, as is called for by the National Forest Management Act.

5. Fish are quickly dismissed (pg m-10) from this assessment with reference to FEIS Chapter 3. As a reviewer, I would like to read Chapter 3 to judge the validity of this dismissal.

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Quality of Information

Most of these analyses involve the distribution of productive old-growth and likely cutting patterns. No mention is made of how the old-growth data set was developed. Hence, I cannot judge its quality.

It was also not clear how harvest patterns were projected into the future. How well was the likely spatial patterning of future harvests factored in? This will strongly influence the spatial patterning of the remaining old-growth. More information on methods here would have been helpful.

Finally, this analysis does a good job of quantifying current and possible future old-growth abundance, but the link between old-growth and species viability is poorly developed.

Conclusions and Recommendations Made in *Appendix M*

The results in this document seem of great importance. They indicate that none of the management alternatives in the forest plan are compatible with the Interagency Strategy in some provinces. This suggests that all the management alternatives fail to have a high likelihood of maintaining well-distributed viable populations of vertebrates. Clearly, the current list of management alternatives should be supplemented with some new alternatives that are more conservation oriented.

Document 3: *Habitat Capability Models for Wildlife in Southeast Alaska*

General Approach

There is much to be said for linking wildlife habitat models and GIS to map current habitat suitability. The Tongass is to be commended for taking this approach. The approach is even more valuable when vegetation simulation models are used to project change in habitat suitability under the different management alternatives. Apparently, this was done to some extent in the Tongass forest plan, but we were not provided this chapter and I cannot comment on it.

Insufficient data is typically a core problem in developing wildlife habitat models. The habitat capability approach is especially useful when data are few and educated guesses must be coded into the habitat models. *Appendix M* nicely reviews the shortcomings of this approach. However, I feel it is important to use

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the best information available, however poor those data may be, rather than to ignore wildlife habitat needs.

When good information is available on habitat use, more quantitative methods of modeling habitat are preferable to habitat capability models. Multiple regression, logistic regression, classification and regression trees are but some of the statistical techniques that have been used successfully (Verner *et al.*, 1986). I think that these approaches would provide better results for some of the Tongass MIS species (e.g., the bald eagle) than habitat capability models.

Overall, the Tongass has done a poor job of implementing the habitat capability approach. As indicated below, best available information was not used for most species, little effort apparently was made to enter into GIS the key data that are needed for some of the wildlife models, the validation effort is virtually nonexistent. The impression I get is that the effort was understaffed, underfunded, and considered a low priority by the forest.

Information Used

The models for individual wildlife species differed dramatically in how well they took advantage of available information. The brown bear model is an excellent example of using both quantitative data and educated guesses to derive habitat functions. The bald eagle model, on the other hand, made very poor use of existing data. The US Fish and Wildlife Service has compiled an extraordinary data set on eagle nesting habitat in the Tongass. This data set could be used to develop very high quantity statistical functions. Instead the habitat capability model effort did no original analyses. More surprising, the model failed to include some of the most important habitat variables reported in the eagle publications (shore characteristics), because that data layer was not yet in GIS. Another problem with most of the species models is that they were completed 3-4 years ago and are now very dated in the literature they used. For example, the results of the recently completed study of breeding bird habitat use on the Tongass were not even used in the models.

Model structure

I agree with *Appendix M* that it is overly tenuous to predict animal density using the habitat capability approach. The HSI index itself seems the more valuable output variable.

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Applications

The material we were presented with did not include applications of the models.

Validation

The plan for validation described in the document is excellent. Unfortunately, it has been implemented only for the brown bear. This is the major weakness of the Tongass habitat capability effort. Data are available for validating the bald eagle model and some of the songbird models, but this was not done. Beyond using existing data, a whole new suite of studies needs to be initiated to make this modeling effort useful.

All Three Documents

The relationships among these documents is very unclear. What role, if any, does the Interagency Strategy have in the Tongass forest plan? It would seem appropriate to include the strategy as one of the management alternatives in the forest plan. Given that this is not the case, why does *Appendix M* use the Interagency Strategy as a benchmark for comparing management alternatives? Why is the viability analysis (*Appendix M*) in the forest plan relegated to an appendix rather than being a central part of the plan? Why are the habitat models ignored in *Appendix M*? Clearly, these three efforts need be merged to produce good products.

3. Species Review - Bald Eagle

The habitat capability model for the bald eagle is woefully inadequate. This is unfortunate because this species has been very well studied on the Tongass and has quite specific breeding habitat requirements. Thus it is a species that is relatively easy to model.

The extensive data set on this species compiled by the US Fish and Wildlife Service could have been much better used. First, the model does not include all of the variables found to be important in the Fish and Wildlife Service publications on eagle breeding habitats. Variables on shore type were omitted, apparently because they were not in the GIS. Information on topography and shore type could have been derived from existing data bases (digital elevation models) and by aerial photo interpretation.

A more important shortcoming is that the Forest Service did not take advantage of the opportunity to reanalyze the Fish and Wildlife Service data set

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in order to develop habitat functions. Very nice multivariate statistical functions could be developed from the data. Instead, the model builders ranked habitat capability rather arbitrarily. For example, western hemlock forests are known to be less preferred for nesting than Sitka spruce forests but there is no basis for assigning hemlock forest an index of .5 (rather than some other value less than 1.0). It is also not clear that the capability indices were based on eagle habitat preference data (as is most desirable) rather than habitat use data. The brown bear model is a good example of using preference data.

The means of predicting eagle density from habitat capability is very tenuous. Nesting density of bald eagles in southeast Alaska is probably more a function of food availability than nesting habitat (Hansen, 1987). Food availability (nor correlates) are not considered in the habitat model. Thus it is unreasonable to predict eagle density based on nesting habitat. The model goes even further off-base in estimating total adult eagle density based on nesting habitat and an average ratio of nonbreeding to breeding adults. Nonbreeding adults have very different habitat use from breeding eagles (Hansen and Hodges, 1985).

In sum, this habitat model is likely to be misleading. Much better models could be developed with the data available.

4. Comprehensive Recommendations For The Future

Conceptual Approaches

Multiple use agencies like the TNF would do well to carefully evaluate adaptive management approaches. The rationale and implementation of adaptive management is described in FEMAT (1993) and Jensen and Bourgeron (1993), and Hansen *et al.* (1993) illustrates an application for wildlife management. Adaptive management gives a construct for organizing and coordinating planning, inventory, research, management implementation, and monitoring. The review documents make clear that the Tongass would do well the better we link these types of activities.

The Tongass is an excellent setting for developing new inventory and monitoring methods for fish and wildlife. The forest is very large, it supports a large number of species, most species are little studied, and several species operate at the landscape scale and will be difficult to manage. New, cost-effective methods are needed that are hierarchically organized, gathering relatively inexpensive, course-scale data on most species, and increasingly fine-scale data on species most at risk. Considerable thinking is needed on the types and scales of habitat variables to measure, and on how to link habitat analyses with demographic analyses.

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New organizational and funding structures may well be needed on the Tongass to meet the requirements of the National Forest Management Act (See FEMAT, 1993 ch. 8).

Suggested Steps for Managing Species Viability on the Tongass

1. Objectives. Carefully evaluate and clearly state the goals for species management on the forest. Include operational definitions of terms like "viable" and "well-distributed". Clarify the priority of these goals relative to those of other resources. Be specific enough in the goals so that there are grounds for objectively assessing how well the goals are met through time.

2. Develop conceptual models and data bases. Assemble conceptual models of the factors that likely control species viability and the scales at which these operate. Vegetation, climate, hydrology, geomorphology, human activities, natural disturbance, and other factors should be considered. Compile data bases in GIS of these potential drivers. Decide on whether a "species-based" strategy, an "ecosystem-based" strategy, or both is most appropriate. Review existing literature or initiate research on presettlement habitat and landscape dynamics to offer a context for landscape management.

3. Rank species, ecosystems, or processes in risk to viability. Develop objective ranking criteria to determine which species, ecosystems, or processes are most at risk and merit higher levels of research of management consideration. The Interagency strategy offers a good example of doing this for old-growth associated terrestrial species. In addition to the types of criteria they used, area of suitable habitat across the current landscape should be considered. This can be calculated using the GIS data developed in step two. In the case of species, all vertebrates should be considered.

4. Develop alternative management scenarios. There is good opportunity to develop creative new management scenarios to accomplish multiple resource objectives. Swanson *et al.* (in prep.) offers an excellent example at the watershed scale that merges consideration of presettlement disturbance patterns, risks to water quality, and forest plan objectives. FEMAT (1993) offers good examples of scenario development at the regional scale.

It appears from the review documents that none of the management alternatives currently under consideration on the Tongass offer good hopes of maintaining viability among old-growth in some provinces. Additional scenarios are needed. The Interagency Strategy could well form the basis of a management alternative.

5. Project the likely consequences of each management alternative. GIS, vegetation simulation models, and species habitat functions should be used to

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project the consequences through time under each management alternative. Key response variables include vegetation patterning, habitat suitability, animal demography (for key species), and wood products volume and value. Examples of modeling systems useful for this purpose can be found in Hansen *et al.* (1993) and Hansen *et al.* (in review). The Tongass appears to be on the right track in developing wildlife habitat models and projecting old-growth response to each management alternative (*Appendix M*). These efforts should be consolidated to make realistic, quantitative projections of the ecological, economic, and social consequences of each management alternative. Again, FEMAT (1993) offers an impressive example. The results of such trade-off analyses give an objective basis for choosing a preferred alternative to be implemented.

6. Implement one or more scenarios, monitor responses, and evaluate effectiveness. Each management implementation should be seen as an opportunity for learning. Walters (1986) gives several examples of how to design such implementations as management "experiments". FEMAT (1993) designates "adaptive management landscapes" that are dedicated to trying new management approaches. The Tongass would do well to try a variety of stand, landscape, and regional silvicultural approaches to determine which strategies best accomplish management objectives.

A rigorous monitoring program is essential to determine how well the scenario was implemented and how key resources responded to the scenario. This information should then be used to revise management objectives and conceptual models, update and expand data bases, and verify vegetation and habitat models.

Good monitoring is expensive and difficult. New cost-effective designs are needed. One approach for vertebrates on the Tongass is to use coarse-scale community studies to determine the habitat associations of most species (not unlike the Old-Growth Wildlife Habitat Study done in Region 6). More detailed studies could then be done for species that are rare or otherwise likely to become at risk. Such studies need be fully integrated into Forest Service activities and budgets and routinely carried out over the forest.

Each of the review documents outlines specific research and monitoring needs for wildlife viability. I thought the list was rather complete.

7. Proceed through Steps 1-6 iteratively, with the goal of continually improving resource management.

Changes to Infrastructure and Funding

FEMAT 1993 lists several organizational changes that could improve Forest Service management.

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5. Species-Specific Recommendations For The Future - Bald Eagle

This species is doing well on the Tongass and can be kept in good shape with only a moderate investment in management. The two main determinants of survival and reproduction appear to be food availability and water-side habitat for nesting, feeding, and roosting (Hansen, 1987). Forest Service activities may strongly influence water quality, aquatic and marine ecosystems, and anadromous and resident fish. Intelligent management of aquatic and marine habitats is essential for maintaining a food base for the bald eagle and other piscavores. Maintenance of feeding, nesting, and wintering habitat is also essential. I suggest the following steps for managing this species.

1. Analyze the US Fish and Wildlife Service data base on eagle habitat use and develop a good habitat model to predict habitat suitability under different landscape scenarios. This should be done on a province by province basis to account for local differences.

2. Standards and guidelines should be developed for this species based on known locations of eagle nests, roosts, etc., and based on projected habitat suitability.

3. Areas designated as eagle habitats should be monitored periodically to determine if the standards and guidelines are effective in maintaining eagle habitats.

4. Data being collected by the Fish and Wildlife Service on eagle abundance, adult/subadult ratios, reproduction, and movements should be analyzed annually to monitor population changes. If population declines are detected, research should be initiated to determine the causes of these declines.

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Tongass National Forest
Land Management Plan

Legal Review

by

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1. Background

I am a professor of law, and I have specialized in teaching and research of natural resources and environmental issues for the past twelve years. Previously, for ten years, I was General Counsel to the National Wildlife Federation in Washington, D.C.

My approach to issues of the sort involved in this review is to examine the requirements of existing law and policy, and to examine the extent to which the materials meet those requirements. I have no scientific or biological expertise in wildlife or forestry issues. I do have experience in legislation, regulation and litigation implementing wildlife and forestry laws and policy.

2. General Observations on Laws and Policies Relevant to the Tongass Planning Process

Three major federal laws prescribe planning for the Tongass National Forest: The National Environmental Policy Act (NEPA), the Endangered Species Act (ESA) and the (combined) Forest and Rangeland Renewable Resources Planning Act (RPA) and National Forest Management Act (NFMA).

In relevant part, NEPA requires full consideration of alternatives in the planning process. 42 U.S.C. § 4332(C),(E). The consideration includes even alternatives that are beyond the ability of the agency to implement, e.g., that may require legal, policy or regulatory changes. NRDC v. Morton. They also include alternatives to assumptions based on existing obligations, e.g., existing contracts of sale of timber from the Tongass National Forest. Tenakee Springs v. U.S. Forest Service. In short, under NEPA, planning for this or any other national forest starts fresh, with all options open.

The ESA is intended to protect the ecosystems on which endangered species depend. 16 U.S.C. § 1531(6). The ESA requires all federal agencies to

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ensure that their activities are not likely to jeopardize listed species or adversely modify their critical habitats, 16 U.S.C. § 1536; these protections extend to candidate species as well, 16 U.S.C. § 1533. The ESA also requires federal agencies to exercise their full management authority to conserve all fish, wildlife and plants, 16 U.S.C. § 1534. The ESA, thus, provides both the authority to protect individual species and their habitats, and the authority to plan, proactively, to conserve nonendangered species populations and ecosystems.

The RPA and NFMA provide for the consideration of wildlife and diversity in national forest planning. More specifically, Part 219 of the Forest Service regulations imposes substantive and procedural criteria on Service planning for both wildlife and diversity.

1. § 219.19 requires management "to maintain viable populations of existing natural and desired non-natural vertebrate species in the planning area." The Service is to "insure" that species are "well-distributed" in the planning area; habitat must be provided to support, "at least," a minimum of reproductive individuals sufficiently "well-distributed" to allow species to "interact." Noteworthy in these provisions are the terms "shall" and "must," these requirements are unequivocal and unqualified.

2. §§ 219.26, 27 require the Service to provide for "diversity of plant and animal communities and tree species consistent with multiple-use objectives," a qualified objective. § 219.26 goes on to require "inventories," however, that "shall include qualitative data making possible the evaluation of diversity," and evaluations themselves for each alternative. This informational and procedural requirement is written in absolute terms. "Diversity," in this scheme, is defined as the "distribution and abundance of different plant and animal communities," § 219.3, see also § 219.27(g). It is clear that, with regard to the maintenance of diversity, the preparation of inventories and the evaluation of alternatives with regard to diversity, plant communities are to be equally considered with animals, and vertebrates.

3. § 219.12 requires forest plans to provide for periodic monitoring and evaluation: "At intervals established in the plan, implementation shall be evaluated on a sample basis to determine how well objectives have been met." Based on these evaluations, "revisions" to the plan are to be made. This provision calls for incremental planning, with the opportunity to make early and major adjustments to accomplish, inter alia, such planning goals as viable populations and diversity. As a corollary, this provision appears to preclude major and irreversible commitments whose impacts could defeat these goals.

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3. Application of These Laws and Policies to the Review Documents

To this non-scientific eye, the "*Proposed Strategy*" document appears to be an earnest, if highly cautious, attempt to apply the above-mentioned legal principles to planning for the Tongass forest. "*Appendix M,*" on the other hand, appears to be largely concerned with defensing even the recommendations of the "*Proposed Strategy,*" and does not appear to implement either the spirit or the letter of these principles.

1. Species selection. The selection of "management indicator species" is explained in considerable detail in the "*Proposed Strategy.*" No similar explanation is provided for "*Appendix M,*" which contains fewer species, includes species that are both hardy and abundant (e.g., the Dolly Varden) to the exclusion of ones that are less hardy and abundant, and excludes species (e.g., Goshawk) that, endangered (yet) or not, present viability concerns and for whom the Tongass appears to be important habitat.

The U.S. Fish and Wildlife Service has recently revised its list of "warranted but precluded" candidate species, elevating some to category one. New species for which the Tongass is habitat, as well, have been proposed for listing. An adequate and updated review based on all listed and candidate species seems warranted.

2. Protected habitat identification. The "*Proposed Strategy*" attempts to relate the needs of species populations to minimum habitat sizes, configurations and connections. This attempt seems directed towards meeting the requirements of § 219.19. Dismissing the relationship between habitat and populations as "unproven," "*Appendix M*" adopts instead the measuring stick of the percentage of old-growth remaining, without consideration of locations, altitudes, connections and most importantly, distribution of this habitat. By this device, "*Appendix M*" avoids the necessity to consider the needs, distributions and connectivity of the habitats of any indicator species; indeed, it is hard to see why, under such analysis, consideration of MISs is relevant at all.

3. Risk. The "*Proposed Strategy*" presents a blueprint for the "survival" of its indicator species. It allows no play for recreational hunting, subsistence, non-consumptive user intrusions or catastrophic ("stochastic") events that will reduce survival opportunity over time.

As stated above, "*Appendix M*" does not attempt to relate species needs to habitat in a quantitative way. Instead, it approaches the question of risk by assuming that a greater than 50% loss, province-wide, of old-growth (or in the alternative, habitat units) would pose a "high risk" to survival. Conversely, habitat losses, province-wide or habitat-unit wide, of less than 50% are assumed to present "low risk," i.e., no risk, to survival. This approach hardly "insures" against threats over a long period of time; no person of my acquaintance accepts

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a 49% risk of survival. Significantly, when in a single paragraph at the end of the risk analysis a less (33%) risk threshold is presumed, viable populations of wildlife in several more provinces become jeopardized.

4. Burden of Proof

The following comments will address the issue of "burden of proof" in proceeding with such a plan in the absence of information necessary to evaluate or ensure against the loss of species or biological diversity.

This planning is being conducted under NEPA, which imposes stringent information requirements on federal agencies. According to the regulations of the President's Council on Environmental Quality, regulations that are binding on all federal agencies, "when an agency is evaluating reasonably foreseeable significant adverse effects" on the environment in an EIS, and there is "incomplete information," if this information "is essential to a reasoned choice among alternatives and the overall costs of obtaining it are not exorbitant, the agency shall include the information in the environmental impact statement." 40 CFR 1502.22 (emphasis added).

We may now review Part 219 of the Forest Service regulations for forest wide planning. (See above). These regulations are also law, and as binding on the Service as enactments of the United States Congress.

1. Viable populations. The strongest regulatory mandate is Section 219.19, requiring the Forest Service to "insure" (sic) that species are "well distributed" in the planning area. The term "insure" sets a high substantive and procedural standard. TVA v. Hill, 437 U.S. 153 (1978) (overriding the ESA's analogous standard "to insure" against jeopardy: "This language admits of no exception;" "one would be hard pressed to find a statutory provision whose terms were any plainer."). See also, Resources Limited, Inc. v. Robertson, 9 F.3d 194 (9th Cir. 1993) (reversing a USFS biological opinion concluding no jeopardy to the Grizzly Bear on the basis of inadequate information to support that conclusion.) This same rigor has been applied to "viable populations" decisions under the NFMA regulations. Seattle Audubon Society v. Moseley, 798 F.Supp. 1484 (W.D. Wash., 1992) (were the Forest Service to adopt a plan projecting "low to medium viability," the court would issue summary judgment against such a decision "right now;" "whatever plan is adopted, it cannot be one which the agency knows or believes will probably cause the extirpation of other vertebrate species from the planning area").

2. Diversity. Section 219.26, 27 require the Service to "provide for diversity" of plant and animal species through "inventories" making possible the evaluation of diversity. The adequacy of the Service's "provision for diversity" and of its "inventories" are the subject of numerous administrative appeals of Forest

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Service plans, and of a small but growing number of federal lower court cases. Although in general these opinions have been deferential to the Service's expertise, see Sierra Club v. Robertson, 810 F.Supp. 1021 (W.D. Ark., 1992); Krichbaum v. Kelley, 1994 U.S. Dist LEXIS 1563 (W.D. Va., 1994); Sierra Club v. Marita, 1994 U.S. Dist LEXIS 1710 (E.D. Wisc., 1994), each case is resolved on its particular facts and the full meaning of these planning requirements will not become clear for years. At this point it seems safe to say that, while the goal of "diversity" remains an elusive one for courts to apply, the information required to support diversity analysis will become increasingly high. Courts are far more comfortable enforcing procedural, informational mandates than substantive goals.

3. Other requirements. Other regulatory and statutory requirements also impinge on the Forest Service's proposed alternative, including prohibitions on "high-grading," Section 101(c)(2), Tongass Timber Reform Act, acreage on limitations even-aged management for hemlock-sitka spruce forests of coastal Alaska, 36 CFR 219.27(d)(2), and NFMA's restriction of clear-cutting to "only where...it is determined to be the optimum method," Sect. 6(g)(3)(F), NFMA. This last restriction has recently been interpreted to enjoin even-aged management exception into the rule," Sierra Club v Espy, 822 F.Supp. 356(E.D. Tex., 1993. This court also noted that the proposed even-aged management did not promote species diversity.

In sum, the information requirements of at least NEPA and the "viable populations" analysis of Part 219 appear to be rigorous, as does the substantive requirement that viable populations be maintained and well-distributed throughout the planning area. Threats to populations, and actions that pose threats of not-yet-determined proportions, run a high risk of being held in violation of law. The "diversity" mandates of Part 219 appear to be considerably more flexible, for the moment, but their requirements, too, are evolving rapidly through litigation. Lastly, the Tongass Plan's compliance with other statutory and regulatory mandates appears questionable, which lends support to the need for its reevaluation.

5. Conclusion

NEPA, ESA and RPA/NFMA provide authority to plan for forest management on a broad ecosystem basis, and require full consideration of this approach at least as an alternative management strategy.

RPA/NFMA, further, require planning based on the maintenance of viable populations and of biological diversity (plant and animal) that has not yet been fully implemented.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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1. Background and Philosophy

My early university education, a B.S. and M.S. in game management from Humboldt State College, reflected and reinforced my applied inclinations, having come from a family with a strong utilitarian philosophy of life. Three early influences were the ecologist Charles Kendeigh, Aldo Leopold (his Game Management was the "Bible," but "A Sand County Almanac" has been reread frequently), and Ray Dasmann. Later graduate training was in a traditional midwestern zoology department where issues of vertebrate biology, speciation and evolution were the "hot" topics. The influences here were Darwin, Ernst Mayr, Eugene Odum, and later E.O. Wilson. I was, and still am, a vertebrate wildlife ecologist who is most comfortable working at the species/population level and perhaps a little less comfortable at the community and ecosystem level.

My education and work experience all fostered a strong mechanistic view of the world; causality implied predictability. If we knew enough we could create any scenario we desired because the system was mechanical; all we needed was knowledge to make it work to our whims. That is a bit harsh perhaps; I never really believed the world was that straightforward. A little experience, and a lot of reading, and I realized that events could be causal and chaotic; that is, knowing what causes something to occur does not mean that one can predict what will happen next. Causality does allow one to make predictions, but only on a limited scale; predictions have a short life span on a localized level.

Most recently (the past several decades) I have been impressed with some of the ideas espoused by Charles Warren and his students. Especially applicable to some of the puzzles I have worked on is their concept of a multi-steady state. This idea can be likened to placing a large ball in hilly country. Displace the ball up one of the hillsides surrounding it, and the ball rolls back down to its valley. Displace the ball to the top of a hill and it may roll back or it may roll into a new valley. Whether the ball will ever return to its original valley is problematic given the large number of hills and valleys in the terrain. Additionally, the hills are of various heights and steepness, adding to the unpredictability of the system and

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the "steadiness" of each valley. This idea seems to explain much of the behavior of animal populations: why at times they seem to act "normally" (in a valley we have come to know) while at others they react erratically (moved to a new, uncharted valley).

This view of the biological world has at least several implications for managing wildlife resources.

1) Management plans with a mechanistic base have limited applicability. In the few instances where we know enough of the causal relationships to make reliable predictions, the system is likely to move to another state, which we know little about, leaving us baffled over the failure of the plan. The change is not likely to even be detected (presuming someone is looking for it) for quite some time. Thus, the span of time during which the plan is appropriate is unpredictable. Such plans should be simple, direct and easily modified.

2) Management plans cannot provide predictable outputs, whether it is board feet of timber, hours of recreation, extinctions prevented, or whatever. Management plans should not be written to produce specified levels of products or services. Such plans only guarantee disappointment, economic dislocation, and political upheaval when the promised levels of outputs do not materialize.

3) Linear comprehensive planning as practiced by the Forest Service (and other conservation agencies) is an unworkable approach. The world is not linear (predictable) nor is our knowledge comprehensive (we cannot know all the valleys, nor which one the system will be in next).

4) Humans are a part of the ecosystem and dependent upon it for essential resources. All ecosystems have been and will continue to be altered by humans, yet we still manage as if humans were one thing and nature was something else. At some point we have to figure out how to extract the resources we need and maintain the long-term viability of the system. I do not see us making much progress despite the widely accepted premise of the first sentence. Our current approach to conservation can be described (cynically) as saving the remnants by locking them up!

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2. General Review

Indicator Species

The idea of indicator species plays a major role in management and conservation of wildlife on National Forests, yet the concept probably has only limited utility. The concept of using one species as an indicator of the health of other species, communities and habitats was roundly debated more than 20 years ago, with the debate centered around whether specialists or generalists were best suited as indicator species. No consensus was ever reached; rather the debate subsided when it was realized that animal species were poor indicators except of only very general conditions, e.g., the absence of ducks indicates an absence of wetland, and *vice versa*.

The concept of the niche precludes closely related species from being good indicators of each other. By definition, similarly adapted species cannot occupy the same niche simultaneously. Without knowing the evolutionary history of the entire array of species, it would be quite difficult to specify the relations between the indicator species and the community of ecologically related species. A single prey species may in a few instances be a reliable indicator of predator abundance, yet the instances are too few to utilize as a general conservation methodology.

The selection of indicator species, for the construction of Habitat Capability Models for site planning purposes, lacks a rational ecological basis. The selection of endangered, threatened, sensitive species, and species of high public profile and economic importance as indicator species has more to do with bureaucratic posturing than with ecologically sound management. Selection of indicator species should be based on criteria that reflect directly the intended purpose, not simply as a mechanism to reduce the number of species to be managed. Community and ecosystem management cannot be accomplished solely by species management of a handful of species at one time.

Habitat Capability Models

The notion that the ability of the land to support a species of animal is detectable and measurable is both conceptually and empirically valid. However, the construction of Habitat Capability Index (HCI) models has several serious flaws that severely limits their management applicability. Models must be based on functional relations of an animal to specific components of its environment. Much of the research on habitats of wildlife is descriptive and uses an association or correlation methodology (a use vs. available data analysis to determine habitat selection/preference). Basing HCI models solely on that sort of information is likely to lead to spurious results. Inferring critical components of an animal's environment (habitat) from an understanding of functional relations (niche)

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allows the construction of a model that has a firm conceptual basis. Such models would be "good science" because they would be explanatory and they would provide a basis for developing testable hypotheses. They would also be powerful application tools because of their explanatory powers.

The choice of modelling methodology also seems inappropriate. A linear, numerical modelling approach is an unrealistic way to describe an animal's habitat. Model functions are so rudimentary, and often arbitrary, as to make the outputs of the models questionable. Rule-based models (also known as decision trees and expert systems, depending on their intended purpose) are flexible models, that can incorporate a variety of input formats (continuous to binomial) (Starfield and Bleloch, 1986). Rules are explicitly justified and rules can be readily recast as hypotheses. Addition and revision of rules can easily be accomplished as the system being modeled becomes better understood. These properties of rule-based models lead rather naturally to adaptive management strategies (Walters, 1986).

Proposed Strategy for Old-Growth Wildlife

The *Strategy* is an innovative and bold attempt to apply species, community and ecosystem concepts to applied management. While only a few species were selected for development of the strategy, they were selected rationally and on an ecological basis. The strategy proceeds from firm ecological concepts to specific concerns to development of appropriate applications. It is in the vernacular, good (applied) science. A thorough description and examination of the methodology are warranted to determine the applicability of this approach to wildlife conservation throughout the National Forest System.

There are several weak points at which the system could break down. First, the selection of species is crucial to development of the strategy and an error here could negate the entire effort. Critical species could be omitted because of ignorance: too little known about them to be considered a candidate. Selection of species could also be subjected to arbitrary criteria as has occurred with indicator species. Finally, management actions could become directed at the selected species regardless of the effects on other species in the community because of the tendency for management to be narrowly goal oriented.

Second, the physical boundaries for which the strategy was developed are arbitrarily drawn around the Tongass National Forest. Extensive as the planning area is in this case, some way needs to be found to integrate surrounding and intermingled areas into the planning effort. This problem would be especially troublesome on most National Forests outside of Alaska, and in many cases could negate any planning effort.

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Incorporating the GAP analysis methodology would enhance the conservation strategy, especially in regard to species selection and boundary constraints.

3. Habitat Capability Model For The Vancouver Canada Goose On The Tongass National Forest

This review is based on Version 3.0 of "Habitat Capability Model for Vancouver Canada Goose in Southeast Alaska: Nesting and Brood Rearing Habitat." Two introductory documents were also reviewed: 1) "Development and Application of Habitat Capability Models for Wildlife in the Alaska Region: by Lowell Suring, and 2) "The Role and Reliability of Habitat Capability Models" by Eugene J. Degayner.

General

The value of habitat capability models is greatly restricted as touched on in the two introductory articles. In fact, the restrictions are so severe that one wonders about expending so much energy to develop the models. A quantitative habitat model that does not have the ability to predict abundance is of little use, and its value in planning is likely to be neutral, at best, and possibly negative. The models imply a much greater level of precision than is warranted. Despite disclaimers about the limitations of habitat capability models, their quasi-quantitative structure will be taken to mean a high level of precision by those using the outcomes of the models, i.e. planners and the public. The concept that we should be able to examine habitat and judge its capability to support a species of animal is valid, but the approach being used can be highly misleading.

A qualitative approach, such as those used in rule-based models and decision trees (Starfield and Bleloch, 1986), allows one to scale the outcomes to the level of accuracy of the inputs. For instance, in some cases a model may only be able to report two categories: suitable or unsuitable habitat. In other cases habitat may be reported on a 10 or 100 point scale. The level of accuracy is imbedded in the way outcomes are classed and is derived directly from the level of accuracy of the input variables. The concept of significant figures is directly analogous: measurement accuracy is implicit and results of calculations are dependent upon accuracy of input. Applying the rules of significant figures to habitat capability models would reveal their weaknesses.

Another weakness in habitat capability models is the number of untested, and unjustified, assumptions that are made. Assumptions are necessary but there must be some evidence that an assumption is correct to justify its use. At the very least, evidence must be presented that an assumption is more likely to

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be correct than incorrect; if it cannot pass that minimal test, then the assumption cannot be used. It is often instructive to assess the consequences of an assumption being incorrect; some errors have serious consequences, while others are inconsequential. A formal testing and analysis of assumptions would increase the reliability, and believability, of habitat capability models. Good science demands that assumptions be thoroughly examined.

Finally, habitat capability models are often too narrowly defined and are based on "habitat" associations rather than on an animal's functional relationship to its environment. The model for Vancouver Canada Geese displays both of these weaknesses, and both are unnecessary in this instance.

Habitat Capability Model for Vancouver Canada Geese

This model is narrowly defined in several ways. First, the Pacific Flyway has developed management plans for all populations of geese in the Pacific Flyway, including the Vancouver Canada Goose. While that plan is largely a population management plan, the review for this habitat model ought to at least recognize the existence of the Flyway plan. Better yet, this review ought to say how the two plans are interrelated, or how this model relates to the Flyway management plan.

Second, the life history events, nesting and brood rearing, are too rigidly drawn. While the model must concentrate on habitat with a specific function, what happens before and after is relevant. For instance, in Canada geese reproductive success is highly dependent on stored energy reserves acquired during the pre-nesting period, sometimes as much as a month in advance of nesting. Acquisition of energy reserves is dependent upon food availability, which is a function of the habitat. To assume that other habitat needs are satisfactorily being met is simply to duck the issue.

Thirdly, the review of available information on which the model is based is too narrowly structured; this is by far the most serious shortcoming of the model. An enormous body of information is available on Canada geese and to restrict the review to Vancouver Canada geese in Southeast Alaska is to ignore almost everything that is known about Canada geese. The model is in effect based upon the *least* available information rather than the best.

The review is also too narrowly structured because it is a compilation of literature and not a critical examination and interpretation of literature on Canada geese. Not all observations and interpretations of facts and events reported in the literature are equally valid; some are very solid, some are speculative, and some are wrong. In the review, little effort is made to separate the valid from the invalid. The critical evaluation of the information is essential to the development of a useful model.

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The information review needs to be done with the goal of developing functional relationships between geese and their environment. Vertebrate biology and behavioral ecology have concentrated on elucidating strategies: how an animal accomplishes certain goals. Strategies are ways animals have evolved to overcome problems, problems presented by their environment and the biotic community in which they live. Understanding the habitat requirements of animals means understanding how animals use their environment to obtain food, avoid being eaten, survive, and reproduce. Unfortunately, most wildlife habitat research consists of descriptions of associations of an animal with a few components of its environment (usually plant communities). However, associations by themselves have little explanatory power and hence little predictive value. Using associations to build a habitat model is likely to lead to unsatisfactory results, especially when the associations are restricted to things that have already been measured for some other purpose. For instance, *Vaccium* is a key component of the model for habitat of Vancouver Canada geese, even though there is only reference to its association with nests and one vague statement about its consumption as food. Tree and canopy cover may be of much more importance to Vancouver geese, yet tree cover is not a model component.

Much is known about the predator avoidance strategies of nesting geese and this knowledge can be used to illustrate how a component of habitat capability model might be generated. Predation of eggs is a key problem faced by Canada geese and they have developed a series of related anti-predator mechanisms. The large size of geese effectively precludes them from hiding themselves while incubating, but does provide them with the opportunity to actively defend their nest. Active defense requires the presence of the male close enough to respond when needed but inconspicuous enough to avoid attracting predators; avoidance is always the best defense, even for a large, aggressive bird. The presence of the pair at the nest is usually enough to deter avian predators, although some avian predators are adept at raiding nests when females are on feeding breaks. Most mammalian predators (up to the size of a coyote) can be repelled if the geese have an advantage. Geese gain an advantage by placing their nests on sites that present access difficulties for mammalian predators. Small islands and elevated structures are strongly selected as nest sites by Canada geese; swimming and climbing mammalian predators are vulnerable to attack by geese. While this mechanism (and there are many others) has been observed in geese nesting in open marshes, Vancouver Canada geese face the same problems and will likely use variations of this strategy to reduce nest predation. Trees and snags may be important in providing elevated structures for nests. Males may use trees as lookout posts. *Vaccium* may be inconsequential and in fact may be an impediment; males standing in *Vaccium* could not see approaching predators and could not readily come to the aid of their mates.

Predation by bears presents special problems for Canada geese; active defense is not an option. Most geese nest outside the range of bears but where

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bears and geese co-occur, as for dusky Canada geese (*B. c. occidentalis*) on the Cooper River Delta, geese select areas that are unused by bears. When bears gain access to those areas, predation rates are greatly elevated. Consequently, avoidance of bears is the preferred strategy. Given the prevalence of bears and their patchy distribution on the Tongass National Forest, the presence or absence of bears may be a primary indicator of quality of nesting habitat for Vancouver Canada geese. The importance of bears for nesting habitat of geese cannot be derived from the classical approach to describing habitats. Additionally, this functional approach to determining the important habitat components leads quite naturally to the development of readily testable hypotheses, thus providing a powerful direction for applied research.

The above is intended merely as an example of how understanding functional relationships of animals and their environment may lead to more realistic and predictive models. In many instances the model functions will be speculative, but based on logical extrapolation from documented relationships in other situations. Such speculative model relationships will provide guidance for directing additional research efforts.

Conclusions

Probably the most important step in the modelling process is the critical and integrative review of available information. This step tends to be slighted in the habitat capability modelling process, being a compilation of a restricted domain of relevant information. These reviews should start from a basic grounding in vertebrate biology and behavioral ecology to discern how the particular species overcomes the problems of existence. Strategies employed in specific situations will reveal the critical elements in an animal's environment that constitutes its habitat. However, wildlife habitat research is largely descriptive of associations of animals with various aggregated components of the environment, frequently components that we as humans can see and measure regardless of their value to animals. Consequently, the reviewers must explore and analyze data from the literature to determine the critical elements of an animal's habitat. It is at this first stage of analysis of the literature where experts from outside the modelling team should first be utilized. A properly done analysis of the literature will provide an enlightened basis for model construction.

Rule-based modelling is a more realistic approach than quantitative modelling, given our level of understanding of the relation of habitat to population abundance. In fact, expecting a strict quantitative relation between specific habitat components and population abundance is a naive view of how nature functions. An additional advantage of rule-based models is that they are easy to understand and construct without specialized training, yet they can be as simple or as sophisticated as our understanding of the system will allow. The rules are stated explicitly and hence easily scrutinized by anyone; this feature

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inhibits embedding vaguely understood relationships that generate estimates that falsely appear to be of high precision.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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1. Background

The intellectual background used in this review is that of population biology (including both ecology and evolution) and theoretical and applied conservation biology. I teach advanced courses and do research in the areas of population and quantitative genetics, evolution, and conservation biology. My activities in conservation biology include development of original theories on genetic and demographic risks of population extinction, and applied work in analyzing data and developing and evaluating conservation plans for endangered species and their habitats. I have contributed to population viability analysis and/or conservation plans on the northern spotted owl, Florida key deer, Florida panther, and African elephant. I was one of five solicited nonagency reviewers of the strategy developed by the Interagency Scientific Committee for conservation of the northern spotted owl (Thomas *et al.*, 1990). Dr. G. Mace and I developed categories of extinction risk that served as the basis of criteria that are in process of adoption by the International Union for the Conservation of Nature and Natural Resources (IUCN) and the Convention on International Trade in Endangered Species (CITES). I recently served on the National Audubon Society committee on restoration of the Everglades ecosystem.

My basic philosophy on conservation biology is largely inspired by the pioneering works of Soulè and Wilcox (1980), Shaffer (1981) and Soulè (1986, 1987). My general views and much of my research on conservation biology are summarized in Lande (1988a, 1994) and Mace and Lande (1991).

2. Comprehensive Review

Habitat Capability Models for Wildlife in Southeast Alaska. ("*Models*")

1. A list of Management Indicator Species has been assembled for analysis, including species of birds and mammals with the largest habitat requirements that will adequately represent an old-growth forest ecosystem.

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2. Only the models for bald eagle, brown bear, marten, and Sitka black-tailed deer have proceeded through part or all of the model verification steps of development, and it is these on which this review focuses. Each of these models begins with an informative summary of present knowledge on the ecology, life history and demography of the species.

3. On p. ii-2 the paper by Lymon and Barrett (1986), describing "many pitfalls associated with the use of HSIs", is not listed in the literature cited on p. ii-6.

4. Habitat Suitability Index (HSI) is an important first step in the direction of population modelling. For a given species under a specified management alternative, HSI indicates the carrying capacity, or maximum equilibrium population size that can be sustained in a region. The models are suitably cautious about the interpretation of HSI, in the sense that a low HSI projected under a particular management alternative is sufficient to indicate a problem with population viability for a certain species under that alternative. However, a high HSI does not guarantee that the actual population will be high or even viable.

5. The major weakness of HSI is that it fails to account for many factors of population dynamics that are potentially important for population viability. Potentially important factors that are only partially accounted for, or completely absent from HSIs, include the effects of habitat fragmentation and edge effects on migration and dispersal, losses due to hunting and trapping, and the effects of demographic and environmental fluctuations on population size and distribution. In some cases only a single limiting factor is identified and included in the HSI, i.e. late summer habitat for brown bear (p. I-8), and winter habitat for marten (p. J-2) and Sitka black-tailed deer (p. L-4), although it is acknowledged that other factors, such as quality of summer forage for Sitka black-tailed deer, have a major influence on reproduction and survival. Thus the approach of HSIs make them intrinsically optimistic, and they may often be poor indicators of population viability.

6. HSIs are of no practical utility unless they have been applied to evaluate habitat suitability for particular species in particular areas under specified management alternatives. Even for the brown bear model, which is nearly completed, I did not see any such evaluations.

A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated With Old-growth Forests in Southeast Alaska. ("*Strategy*")

1. This is a good initial attempt to develop a strategy for maintaining overall biodiversity. This *Strategy* considers multiple species, focusing on birds and

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mammals with the greatest and/or most specialized habitat requirements, which are likely to represent the old-growth forest ecosystem. It is not clear why the bald eagle was excluded from the list.

2. The *Strategy* is based on the Habitat Conservation Area (HCA) concept developed by the Interagency Scientific Committee for conservation of the northern spotted owl (Thomas *et al.*, 1990). Thomas *et al.* (1990) relied on observations on viability of small populations of birds, on modelling, and on general considerations of edge effects to suggest that HCAs should have a target size of at least 20 breeding pairs of owls to greatly reduce local extinction rates. It is clear that large blocks of undisturbed habitat are a desirable component of any plan to maintain biodiversity, since they reduce fragmentation and edge effects. In the *Strategy*, large HCAs composed of 20,000 contiguous acres of old-growth (containing at least one class I anadromous fish stream) are stated to be capable of supporting 8 pairs of goshawks, 5 female brown bears, and 25 female marten (and perhaps during winters poor prey (*Strategy* p. 27). There is no observational evidence or modelling cited for any of these species to suggest that these numbers will adequately reduce local extinction rates. Such small populations of brown bear (with fewer males than females) and goshawk would be subject to strong effects of demographic stochasticity and possible inbreeding depression, and the same may be true of marten in which population densities are known to fluctuate substantially among years because of changes in prey abundance (*Strategy* p. 210). In addition, for the species with long dispersal distances, dispersing individuals may spend considerable time wandering through unsuitable habitat searching for suitable unoccupied habitat in which to establish their home range. This effect of fragmentation may cause a substantially increased juvenile mortality, thereby lowering population viability. The *Strategy* commits the same error as in the HSI Models by assuming that all suitable habitat will always be fully occupied by each species, and that dispersal provisions are fully adequate, which may not be valid for any of the species. See suggestion 5 under Comprehensive Recommendations for the Future, Philosophical and Conceptual Considerations.

3. The spacing of large HCAs no more than 20 miles apart is determined by considering distributions of individual dispersal distances for the species, and is likely to be within the typical dispersal distances of most individual brown bears and goshawks. Medium HCAs including 5,000 acres of old-growth are supposed to be capable of supporting at least 2 pairs of goshawks and 5 female martens during winters of poor prey (*Strategy* p. 28), and are to be spaced no more than 8 miles to the nearest other medium or large HCA. Small HCAs including 800 acres of old-growth are supposed to be capable of supporting at least 1 female marten in winters of poor prey (*Strategy* p. 29) and are to be located at least one per major watershed (≥10,000 acres). Medium and small HCAs and travel corridors consisting of 500 ft beach buffers and 100 ft riparian buffers, and additional travel corridors deemed necessary at the project level, are supposed to be sufficient for dispersal of species dependent on old-growth. There is no

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evidence that such narrow corridors surrounded by heavily disturbed habitats (such as clear-cuts) would be effectively used by the species of concern, and if they are, that they would not be subject to serious degradation by edge effects including erosion and wind throw. Data on p. 187 of the *Strategy* appear to indicate that habitat up to at least 200 meters of anadromous fish streams is heavily used by brown bears in late summer. Only a few small gaps in such a corridor could constitute a serious barrier to dispersal for small species such as marten or flying squirrel. I question whether this *Strategy* is likely to maintain viable well-distributed populations of most old-growth species. See suggestion 6 under Comprehensive Recommendations for the Future, Philosophical and Conceptual Considerations.

4. Thinning of second-growth, and salvage logging within HCAs and within narrow riparian and seaside buffers should not be allowed. These activities are likely to produce detrimental effects, including compaction and erosion from road building and movement of heavy machinery, destruction of snags and removal of future down woody material that are important to numerous old-growth species.

5. Brown bears are the only species for which any population modelling was done. The program used, POPDYN4, is poorly suited to population viability analysis because it assumes no density-dependence and no environmental stochasticity. It also has no spatial component and therefore cannot deal with edge effects, dispersal and migration, or habitat heterogeneity or fragmentation. The results therefore tend to be overly optimistic and have limited value for conservation planning.

Appendix M. Fish and Wildlife: A Viability Risk Assessment. ("*Appendix M*")

Appendix M is frank about its assumptions and limitations. It assumes (p. 20) that the HCA *Strategy* will insure viable populations of all Management Indicator Species, which has not been demonstrated, and may be overly optimistic. It assumes (p. 20) that an HCA is completely nonfunctional if the amount of old-growth it contains is reduced below the minimum specifications or initial amounts (whichever is smaller), which is overly pessimistic. It adopts arbitrary measures of impact on population viability based only on habitat, such as percent of 1954 productive old-growth within an ecological province, and percent of large and medium HCAs affected within a province. No attempt is made to analyze risks on a species specific basis, even using HSIs, much less population dynamic models. This is not a valid approach to viability analysis for any particular species.

The main conclusion of *Appendix M* is fairly obvious: any ecological province in which the vast majority of productive old-growth is eliminated has a high risk of not maintaining viable populations of species dependent on old-

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growth. These provinces form a nearly contiguous block in the south-central part of the region. This analysis has identified regions of extremely high risk but may have failed to identify other regions with substantial risk for some species.

3. Comprehensive Recommendations for the Future

3.1 Philosophical and Conceptual Considerations

1. Quantitative PVAs are needed for at least a few key species, incorporating population dynamic effects of habitat fragmentation on migration and dispersal, and the effects of demographic and environmental stochasticity. These should include a range of models incorporating temporal and/or spatial effects, from analytical models (Lande, 1987, 1988b, 1993), and computer simulations (Doak, 1989; Lamberson *et al.*, 1992), to GIS models of habitat, and ultimately spatially explicit GIS-based population dynamic simulations (McKelvey *et al.*, 1993).

2. Management should be adaptive and willing to change its goals as new information is acquired. Population modelling and gathering of demographic data should be done simultaneously. If local data on reproduction, mortality and dispersal by age or developmental stage is not available, initial models could be based on demographic data on the same species from other areas or on data from closely related species. Sensitivity analysis of the models will help to identify which parameters it is important to know most precisely to make accurate predictions, and it is these on which field work should be focused.

3. Population viability models for species with long generation times, such as brown bears, should have time frames longer than 100 years because populations of such species may show gradual long-term declines with a low probability of extinction within 100 years but a high probability of extinction on somewhat longer time frames.

4. The reason for excluding anadromous fish from all of the documents is unclear. *Appendix M* (p. 10) states that there are no anticipated impacts on anadromous fish. However, intensive timber harvesting in some ecological provinces may produce significant erosion and siltation effects and cause alteration in stream flow patterns, which could have cumulative negative impacts on spawning beds.

5. To ensure viable well-distributed populations of all Management Indicator Species may require at least one very large HCA within each ecological province or island. To eliminate most edge effects, including dispersal of individuals across large tracts of unsuitable habitat if narrow buffer zones are not used as dispersal routes, this very large HCA should have a diameter larger than the average individual dispersal distance. Because the Tongass is naturally

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highly fragmented with major ocean barriers between islands that effectively prevent dispersal by terrestrial species, at least one very large HCA on each large island may also be necessary to maintain viable populations of some species. I am especially concerned about the low actual (and effective) population sizes of brown bears on Baranoff and Chichagof Islands that would be maintained under the *Strategy*, which would reduce them to a level that may require their listing as threatened or endangered.

6. The spider web of narrow riparian and beach buffers may be inadequate to promote effective dispersal among HCAs in the *Strategy*. I recommend one of the following two alternatives: (1) large and medium HCAs should be connected by wider travel corridors (e.g., 1000 ft from center to edge), with additional buffer zones around them (e.g., only light selective logging and little or no roads or other human disturbance for another 1000 ft surrounding the corridor), or (2) riparian and beach buffers should be combined with a managed matrix approach such as in Thomas *et al.* (1990). This second alternative would be facilitated if clear-cutting were replaced by selective logging to meet biologically determined matrix standards outside HCAs and buffer zones.

7. The widths of beach and estuarine buffers in the *Strategy* do not account for the predicted global rise of sea level of about two feet during the next century caused by global warming. Along shores with shallow slope the width of seaside buffers may need to be increased, after accounting for current rates of sea level change due to local tectonic processes and prehistoric changes in glaciation (land rising or falling). Likely changes in regional temperature and precipitation patterns due to global warming should also be taken into account in developing long-term conservation plans.

8. Long-term management strategies should be conservative, in the sense of being designed to maintain ecosystem function, rather than to maintain minimum viable populations of chosen species. This is especially true of systems based on slowly renewing resources, such as old-growth forests or animal species with long generation times, because by the time evidence has accumulated to establish continued population decline it may be too late to reverse the process and recover the habitat and the animal population to a viable state. In other words, "adaptive management" of such systems should allow for long time lags in response to changing management decisions.

9. Long-term timber contracts are the logical antithesis of adaptive ecosystem management. There are a few obvious solutions.

10. Hunting and trapping quotas for game species should be set yearly on the basis of estimates of current and projected population sizes, including incidental and illegal take, so as to minimize the risk to population viability for a given average level of hunting or harvesting pressure. Generally, even in the case of maximum sustained yield harvesting, this will involve a zero quota in years

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when the population falls below a size not much less than its stable equilibrium or average size in the absence of hunting or harvesting (Lande *et al.*, 1995).

3.2 Research and Monitoring

1. Genetic studies of introduced marten populations on different islands with known founder history might provide information useful to their management. This would include studies of allozyme polymorphism and possibly mitochondrial DNA polymorphism. It might also be feasible to perform some captive breeding experiments to measure inbreeding depression in marten. Depending on the results, it might be advisable to augment the gene pool of some of the introduced populations to increase their genetic variability.

2. Intensive monitoring of selected Management Indicator Species, and all game species, should be done at least a few times per generation, if not yearly, to detect changes in population size, age distribution, and declines in reproduction or juvenile survival. Mechanisms should be developed to input this information directly into population models and adaptive management feedback loops, for setting harvesting quotas on game species and for determining locations and amounts of allowable timber harvest.

3. Monitoring of ecosystem function should also be done, including biological and physical factors. Variables to be monitored could include forest regeneration rates, soil organic matter and microfaunal composition at regular times after timber harvest at different types of sites and under different harvesting regimes, as well as stream flow patterns, suspended silt load and nutrient concentrations of selected streams in watersheds with different amounts of timber harvest.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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1. Background

My background is as an ecologist and vertebrate biologist with over 40 years of professional experience. My specialty is the population biology of small- and medium-sized mammals, but I maintain an interest in all aspects of land use planning, wildlife management, and conservation. In the last 15 years or so, my research interests have been increasingly focussed on the spatial structuring of populations, meta-population dynamics, and landscape approaches in mammalian ecology. Relevant undergraduate courses that I teach are: principles of ecology, vertebrate natural history, mammalogy, and foundations of conservation biology.

My philosophy with respect to national forests is that they should be managed for multiple use in a sustainable fashion. That is, timber harvests should be sustainable and the biota should be sustained or enhanced but not diminished over the long term. This view is, I believe, consistent with current Forest Service policy as required by the National Forest Management Act of 1976 along with subsequent implementing regulations. The survival of human civilization depends on a healthy biosphere which in turn is inevitably diminished by losses of species, locally and globally. Finally, I believe that utilization of land for education and/or expansion of human understanding and knowledge should be viewed by planners as an extremely valuable use and one that is important in contributing to the sustainability of the human species.

2. Comprehensive Review

The planning strategy outlined in the three documents provided ("*Strategy*," "*Appendix M*," and "*Models*") presents laudable objectives that are based, with a few exceptions, on sound biological principles, and proposes a defensible land use plan based on these objectives. The plan, however, is deficient in my view in several important respects, as I will detail below, and

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improvements should be made. Much more critical, however, is the fact that the timber harvest plans, only occasionally alluded to in these documents, seem to be incompatible with and uncoordinated with the Wildlife Strategy. To the extent that this impression is true, the timber harvest plans are legally and morally unacceptable. Obviously, any strategy for sustaining the biota is meaningless unless it is an integral part of a strategy for sustaining the timber harvest.

Managing the Tongass Forest shares several important features with other boreal rainforests such as in coastal Oregon and Washington. These forests have the special feature that in climax form (old-growth) the trees are relatively old and relatively large. This is critically important because it means that 1) it takes a very long time for succession to reach the old-growth stage, at least 250 to 300 years and perhaps 500 to 600; 2) successional stages (second-growth) are very unlike the climax stage for a long period of time (at least 250 years in the case of the Tongass) whereas in other forests second-growth may closely resemble the climax in only 50 to 100 years; and 3) organisms adapted to old-growth are less likely to be able to utilize second-growth within a typical harvest rotation scheme of 100 or less years. These important features of boreal rainforests means that timber harvest strategies must be qualitatively different from those in forests where succession takes place in a time period more amenable to ordinary human planning efforts. Moreover, a much larger percentage of a boreal rain forest must be in a climax form because, as pointed out, there is a reduced ability of the fauna to adapt to second-growth. How big a percentage will depend on how big the total forest management area is, the requirements for maintenance of viable populations of the largest and most area demanding of the included biota, and on how skillfully a meta-community of old-growth patches is designed. In the case of the Tongass, this might be about 50% (34.2% actually proposed in the *Strategy* document) because of the existence of several area-demanding species (goshawk, brown bear, and gray wolf), the pre-existing clear-cutting of large amounts of old-growth forest (11% by 1991; Table 2, p. 52), and the island archipelago nature of the Tongass Forest.

The constraints outlined make forest block rotation harvesting impractical and inefficient. If it takes 300 years to reach climax condition and 50% of the total area must be in climax at any one time, annual harvest would be limited to (1/2 x 1/300 = 1/600) 0.167% of the forest (9400 ac). This means that in the 37 years from 1954 to 1991 only 0.59% of the forest should have been harvested. In fact 18.6 times that much was actually removed. Honest management utilizing a rotating block design as seems to be implied in these documents (*Strategy*, p. 10), would therefore require that no trees be harvested for 19 years, after which harvesting could be resumed at the rate of 0.167% per year.

The obvious alternative that would supply a much larger sustainable yield of timber is to establish a meta-community of old-growth patches carefully designed to conserve the associated biota totaling about 50% of the 1954 old-growth. The remaining 50% could then be harvested all in one year, if desired, in

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which case no further tree cutting could take place until the second-growth that resulted was harvestable. Or, the harvestable 50% could be cut gradually over a much longer period. The intelligent tactic would be cut the available old-growth as slowly as the national demand for old-growth products would allow, and in any case at a diminishing rate as increasing amounts of second-growth became harvestable. Such a conservative policy would also allow time for the meta-community design to be tested for effectiveness, and possibly modified if necessary (adaptive management). If all the harvestable old-growth were removed in one or a few years, managers would have to assume that their meta-community design was workable, because no changes would be possible within a 300-year time frame.

One unique feature of the Tongass Forest that adds to the complexity of management planning, but also adds significant value to the forest beyond its commercial value for wood, is that it is located on an island archipelago. All biologists are aware of how critically important island archipelagos have been in fostering ecological and evolutionary theory. Incredibly, the Alexander Archipelago has been little explored and its potential for contributing to basic research is unknown, but potentially great. The existence of a large array of islands of various sizes and levels of isolation, most relatively unmodified by human development, is a tremendous asset to biogeographers, ecologists and evolutionary biologists, and by extension to humanity as a whole. There is no evidence in these planning reports that Forest Service biologists have been systematically documenting the biota on these thousands of islands in their care. There is no HCA on Annette Island which is the source of the only record of *Batrachoseps* north of Washington.

Some hint of the extraordinary nature of the Forest's biota is suggested by the large number of subspecies of mammals that have been described for these islands. Some of these named taxa are undoubtedly invalid, but their existence suggests that detailed studies of a number of species is overdue. Only a month ago a revision of the *Peromyscus* from this coastal region was published (Hogan *et al.*, 1993) that makes major changes in the taxonomy of this group, and suggests that at least five subspecies of *P. keeni* may occur in the Forest. In addition there are two to four subspecies in six species of microtine rodents described from or suspected to occur in the Forest. The status of the endemic species *Microtus coronarius*, known only from Coronation, Warren, and Forrester islands is unknown and unacknowledged. *Mustela erminea* has five subspecies described for the area, and *Sorex vagrans* three. *Ursus arctos* has 13 named forms described for the archipelago, none of which is probably valid, but they suggest along with the other polytypic species that some very significant evolutionary studies remain to be done in the area. None of this important and interesting biotic complexity is given any importance in the existing management plans.

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A third general criticism is that the reports do not address interactions between the marine environment and the forest management strategy. Such interactions are clearly relevant to the salmon runs which are not only important in their own right, but also are critical components in the sustainable management of several of the vertebrate management indicator species (MIS). Also contained within the Forest's jurisdiction are marine areas utilized by eight species of endangered whales and one species of threatened pinniped (Steller's Sealion). Appropriate Forest management must address potential interactions with these species.

Aside from these three general faults in the Forest's planning strategy, how well does the proposed Wildlife Strategy accomplish its objectives? The strategy outlined is a giant step in the right direction, but improvements are needed to make it conform to its stated objectives and to the law. Here are some general criticisms.

1) The habitat conservation areas (HCAs) are laid out so as to minimize the impact on timber harvest (*Strategy*, pp. 5, 6, 23, and elsewhere), and not so as to optimize the old-growth meta-community that is required to conserve the area's biota (Appendix I). Most of the large HCAs (63.2%, and not the claimed 25%, *Strategy*, p. 36) are largely or wholly in designated wilderness or other areas presumably unavailable for timber harvest. Moreover, the HCAs within protected areas are generally the largest. This means that whereas the average HCA size fits the prescribed minimum sizes, most of the new HCAs do not (71.4% of the large and 50.0% of the medium). This is not trivial, because the minimum sizes of HCAs are based on minimal requirements for viable populations, and therefore average size is not an adequate measure of adequacy. To be effective, every HCA must meet minimum requirements. It is also clear that the HCAs proposed are not viewed as permanent reserves (e.g., *Strategy*, p. 38), as most are projected to decline in value over time with scheduled timber harvesting. This is clearly an unacceptable feature of the plans.

2) Almost no attention is given to management of the matrix, that is to the forest outside of the projected reserves. Buffer zones along water ways and coasts are clearly important to the success of the plan as well as to the successful conservation of several species of special concern. But, this is not enough, because some HCAs do not appear connectable by such corridors. In such cases timber harvest should be organized so that strips of second-growth of various ages can be used by organisms to disperse between HCAs. This neglect is especially evident because distances between HCAs are based on <u>maximum</u> known dispersal distances of the generally large and mobile species of concern (*Strategy*, p. 221), and no attention is directed to dispersal of all the rest of the biota, which also must succeed in the planned meta-community. Moreover, the proposed gaps between HCAs do not seem to take topography into account. A three-dimensional view of the intervening terrain between HCAs is important in evaluating the efficacy of dispersal among them. It should also be pointed out

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that a variety of recommendations are given for the appropriate widths of the riparian and coastal buffers (ranging from 100 (p. M-13) to 1000 feet).

A few specific comments follow:

page 10 - Removal of old-growth up to 1991 is claimed to be 6.7% here and 11% on page 52.

pages 15, 17, and Table 3 - Suggest that criteria 4 and 10 should have a weighting factor of 5 as these are among the most critical factors in extinction proneness, but that the level of concern for these criteria could be low if the species are widespread within the Forest.

page 19 and Table 3 - Criterion no. 14, pre-fragmentation abundance, may be a misleading predicator of post-fragmentation persistence (Laurance, 1991).

page 22 - A "loosely constructed" conservation plan is okay as long as adjustments are not thwarted by irreversible old-growth harvests.

page 25 - "high likelihood" is a slippery standard for this fundamental goal.

page 26 - The recognition that game species and fur-bearers might be required to provide some harvest to humans and hence must be managed for numbers above mere survival levels (paragraph 2) is not incorporated into the Conservation Strategies.

page 27 - Many of the proposed HCAs do not meet minimum standards for brown bear and gray wolf. Twenty miles is not the dispersal capability of <u>all</u> the species of concern as claimed since the objective should be to conserve the entire old-growth community. Monitoring of large HCAs is commendable but where in the plans is any thought given to what options will remain viable if improvements are needed? See comment on lines 5-7 and end of paragraph 2 on page 41.

pages 31-36 - These "Additional Standards" are loaded with qualifiers and exceptions.

page 32 - Why is it assumed that Great Blue Heron nest sites abandoned for two years will not be re-used? What is the logic of prohibiting timber harvest and road building within 220 m. of heron nests during the breeding season, but allowing it at other times?

page 33 - What is the evidence that only 10% of a shoreline is accessible to skiffs?

page 40 - The "conclusion" of not allowing species extinctions or local extirpations is stated only as an objective, and is clearly not a conclusion of the

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plan as Table 15 (page 81) shows only 7 out of 21 provinces having a "medium high" or better chance of succeeding by 2140.

Appendix M

Table M-1, page 14 - This table is partly illegible. How is it that two provinces are listed as having 100% of their area protected and yet have old-growth available for harvest listed at 22 and 10%?

page M-16 - Choice of these five species for conservation strategies may be adequate for determining size of HCAs, but does not address the dispersal needs of other species. Also habitat requirements for goshawks and martens do not include the criterion of salmon streams for bears.

page M-20 and Figs. 3-18 - The whole concept of HCAs being susceptible to timber harvest violates the basic foundations of any viable meta-community plan. Note that 8 of 21 provinces already have more than 50% of their proposed HCAs affected by harvesting (see Fig. M-3).

3. Species Review

I was not asked to review any particular species management plans, so I looked at them all paying especial attention to the mammals. First I have two general comments.

1) There are four large mammal species whose distributions likely extend into the Tongass Forest, but that are not mentioned in the report. The first two would definitely use old-growth forest as their primary habitat. These are:

wolverine (*Gulo luscus*)
fisher (*Martes pennanti*)
caribou (*Rangifer tarandus*)
moose (*Alces alces*)

2) The Habitat Capability models as presented ("*Models*") and as utilized in the "*Strategy*" suffer from two conceptual weaknesses. The first is that species interactions are difficult to include, other than with those species that enter into the habitat description itself. To some extent this was handled by considering patches with and without some other species present, e.g., wolf. The second flaw is the failure to incorporate landscape features into the model. This problem is not acknowledged explicitly in the reports, but in at least three cases the importance of juxtaposition of two different habitat types was pointed out. One case was the need for brown bears to have access to salmon streams adjacent to old-growth forest, the second was a requirement for otters to have streams with

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certain properties next to forest of appropriate type and elevation, and the third was the importance of escape cliffs in proximity to feeding areas for mountain goats. It is in fact frequently the case that species will require several different habitat types either simultaneously or over the course of an annual cycle. Often these life history features were mentioned in the narrative descriptions of the various species, but generally got lost when the habitat capability models were developed. The results are especially misleading when each habitat-type is presented as supporting a particular density of individuals. Suppose, for example, that one focal species was found to have a density of nine in habitat A and one in habitat B. The obvious conclusion would be that A is this species habitat and B can be safely eliminated. It may be in fact that our species requires both habitats A and B but spends 90% of its time in A and only 10% in B. In this case eliminating B would cause extinction of our focal species.

Comments on Species Plans

Gray Wolf: page 161-2. It seems incredible that in a national forest 14.6% of the population could be harvested each year when the species is legally protected.

Black Bear: No mention of interactions with Brown Bears. Tables 1, 2, 4, 5 do not acknowledge that bears move among habitats and that proximity of various habitats may be critical. Footnote "b" in these figures is not understandable.

Brown Bear: No mention of interactions with Black Bears. Table 3 has the same limitation as the four tables above. A streamside buffer of 100 m. wide is recommended (p. 187) when the data suggest this should be 200 m. The bear's value as a game species is mentioned but the HCAs proposed are inadequate even for survival (see viability analysis for Chichagof Island, p. 181 and Fig. 3).

Marten: This chapter has the highest concentration of typos and stylistic errors of all the chapters. Conservation strategy as defined (p. 206-7) does not take "interaction" to mean movements between watersheds, and this is a serious flaw, because movements are an essential component of any successful meta-population. Pages 208-9: capitalizing americana is very unprofessional. Distance between HCAs is based on the maximum recorded dispersal distance (p. 221), and without regard for the nature of the matrix (p. 215). Discussion of interspersion of habitats (p. J-6) is excellent, but this information is not used later in habitat models (Tables 1, 2, 3, 4).

River Otter: I am surprised that harvesting is at the rate of 500 trapped in 1989/90 and yet the population is thought to be stable or increasing.

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Black-tailed Deer: Fig. 1. How is it that a habitat patch of 0-size still has an effectiveness of 0.30?

Mountain Goat: It is illogically argued (p. 244-5) that because populations of *Ovis* decline rapidly to zero if less than 50 and persist for 70 years if at 100, that mountain goat populations on the Tongass should be left alone if less than or equal to 50, and reduced to 50 if initially greater than this. This is a sure formula for disaster.

Northern Flying Squirrel: Page 252, bottom paragraph: It is a non-sequitur that a food resource that cannot maintain a species is probably unimportant to it. We would not last long on a diet of 100% salt, but it would be stupid to conclude that salt is unimportant to us. Similarly, the conclusion that these squirrels eat only lichens and fungi is contradicted by the strong attraction they have to peanut butter or prunes as bait. Recommendation that stringers of old-growth may be required to connect HCAs (p. 255) must be transferred into the timber harvest planning.

4. Comprehensive Recommendations for the Future

1) A meta-community should be established that will serve the mission of sustaining the biota of the Tongass National Forest. This is to include an appropriate number, size, and distribution of HCAs along with riparian and coastal buffer zones of about 300 m. width. Sustained harvest of timber must be planned in the areas outside of the meta-community with attention directed to providing the necessary corridors among the HCAs. HCAs might be more optimally arranged as a few large areas, one per island or island group, and not according to the calculated minimum sizes as proposed. Such a strategy would increase the problem of dispersal among HCAs but corridors and effective matrix management could help to alleviate this disadvantage. On the other hand, dispersal among HCAs would be less critical, at least on a regular basis, because each HCA would be large enough to be self-sustaining for all species except perhaps brown bears and wolves.

2) Islands of 5 to 1000 ac. in size should be considered off-limits to timber harvest. Those larger than 1000 ac. should have one or more HCAs established on them. In addition, islands that are unique because of extreme isolation and/or the presence of endemics, such as Forrester Island, should be untouched by commercial timber harvesting.

3) Planning for a sustained biota and timber harvest should take into account the archipelago nature of the Tongass Forest and the potential value this has for future research. At least the known taxonomic diversification within the island group should be accommodated.

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4) A research program directed at documenting the biota of each island in the Forest should be instigated. The most economical way to do this might be to provide small research grants to various university teams of investigators. Voucher specimens should be collected and made available to cooperating systematists.

5) Habitat models need to be developed that take into account the juxtaposition of habitat-types and species interactions.

6) It is important that the timber harvest plan allow sufficient time for the meta-community plan to be monitored and appropriate refinements made. This is the essence of adaptive management.

5. Species Specific Recommendations

1) The status of the four species mentioned in 3-1 above should be determined.

2) Where harvesting of game species is desirable and/or anticipated, the meta-community must be designed to produce the required number of individuals.

6. Other Comments

1) The "spotted frog" is not identified by scientific name anywhere in the documents.

2) The group of indicator species (MIS) seems to be well-chosen except for one caveat. There seems always to be a tendency to choose the large and mobile species which has the advantage that the minimum sizes chosen for HCAs will generally be suitable for other members of the biota. But, such a choice may over estimate the required distance between HCAs. Shorter distances may be required to maintain a meta-population structure for the less mobile members of the community. Without taking such factors into consideration, planners would risk a scenario in which a meta-community plan was suitable for large carnivores and ungulates only to find that critical prey populations became extinct in some HCAs rendering the whole structure precarious. It is probably a good idea to include at least one poor disperser in a group of MIS to alleviate this problem. In the present circumstance, the flying squirrel may serve that purpose.

3) The criteria for choosing MIS (pages M-7, 8) are debatable. Aside from the unprofessional language, I find only four of the 10 criteria appropriate (nos. 1, 3, 5, and 10) on scientific grounds. After all, the objective in choosing MIS is

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to find species that will reflect the needs of the entire community. Only criteria that truly represent those needs should therefore be used.

Appendix I - Analysis of the HCAs
(based primarily on Table 8 in "*Strategy*" and the map titled "Conservation strategy for wildlife habitat")

Large HCAs (n=38)

Located (>50%) in designated wilderness or LUD2 areas - 24 (63.2%)

Located outside (>50%) of such areas - 14 (36.8%)

Size of those in protected areas: $\bar{x}$ = 47,413 ac; range 33,310 - 69,032.

Size of those outside of such areas: $\bar{x}$ = 39,109 ac; range 30,296 - 56,436*.

* - The largest of these (no. 38) has >25% in wilderness areas and apparently contains no harvestable timber.

HCAs having less than the minimum required features:

Size (min. 40,000 ac) - 15 (39.5%), and this includes 71.4% of the HCAs outside of designated protected areas.

old-growth (>25% class 4 and >25% class 5+ required) -
class 4 - 19 (50.0%) have less
class 5+ - 13 (34.2%) have less

Medium HCAs (n=111, 6 of which I could not find on the map)

Located (>50%) in designated wilderness or LUD2 areas - 31 (29.5%)

Located (>50%) outside of such areas - 74 (70.5%)

Size of those in protected areas: $\bar{x}$ = 13,419 ac (range 6,655 - 24,534)

Size of those outside of such areas: $\bar{x}$ = 10,144 ac (range 5,548 - 16,971)

HCAs having less than the minimum required features:

Size (min. 10,000 ac) - 37 (50.0%)

old-growth (>25% class 4 and >25% class 5+ required) -
class 4 - 50 (45.0%) have less
class 5+ - 53 (47.7%) have less

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Tongass National Forest
Land Management Plan

Scientific Review

by

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Here are my main conclusions and suggestions:

Overall, I support the procedure for wildlife species conservation planning taken by the viability committee.

1. Develop rationale for conservation needs. I am not particularly familiar with the content of the current and previous forest plans for the Tongass NF. I don't know what has been proposed in the past for management requirements for management indicator species (MIS) or sensitive species, or the full content of these species lists. If a conservation strategy is deemed necessary above and beyond such in-place management guidelines, or if there are additional species of potential management concern that do not appear in existing lists of MIS or sensitive species, it might be worthwhile to carefully document why this is so. The draft conservation strategy document helps highlight such concerns in its viability screening process. The viability committee might extend this documentation to all species it considered. Also, I had suggested a simple means of assessing such needs for species of particular conservation significance by mapping areas of distributional concern (details below). This could be part of documenting why a broader wildlife conservation strategy is of interest.

2. There is a need for field inventories. There is a strong need for field information on presence, distribution, abundance, trend, and specific habitat associations of most wildlife species on Tongass NF. However, I believe that there is sufficient information available to trigger concern for some species, and to allow us to qualitatively assess the degree of such concern and risk.

I support development of an integrated inventory-monitoring-research program. The program would be designed in part to conduct basic wildlife surveys and to more precisely describe habitats used and selected by key wildlife species. The archipelago nature of Tongass NF is a major challenge to conservation of sensitive and indicator species and their associates. Basic field

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data is absolutely essential for wildlife conservation planning to proceed much beyond the current level.

3. The conservation strategy and the viability committee can contribute in a positive way to forest planning. The proposed conservation strategy would help retain conservation options over the short run -- say, the life of the next planning cycle -- while basic field data are being gathered and validation studies are conducted. I suggested to the viability committee that they fully write out the major assumptions of their strategy approach, as some of them can be tested with validation monitoring studies conducted by Forest Service Research in cooperation with the National Forest.

The viability committee can make a positive contribution to forest planning in Region 10. I conclude this based on my experience in Regions 5 and 6, particularly with planning efforts on the northern spotted owl. The viability committee is precisely the sort of cross-agency collaboration of species experts that I originally called for during the first interregional northern spotted owl EIS in 1985-87. Unfortunately, the time line and line direction precluded forming such a team back then for the owl. As you know, later the Interagency Scientific Committee (ISC) was commissioned under the leadership of Jack Ward Thomas to conduct such functions. Then, the second northern spotted owl EIS has recently been completed; in that effort, we were given full support for convening a viability assessment committee of experts and researchers. In fact, a core team of viability planning experts, which included Marty Raphael and myself, was established as an adjunct advisory group to the EIS interdisciplinary team. This structure worked well.

Ultimately, planning direction certainly must come from line decisions, but development and analysis of conservation alternatives that are biologically defensible really should be generated by such expert panels. In this spirit, I support the concept and work of the southeast Alaska viability committee.

4. The viability committee should be recognized as a partner. The viability committee can be a valuable partner and resource for the Tongass NF LMP process. I would view the current conservation strategy as one alternative that could be analyzed in the forest plan. The viability committee can be called upon to help make clinical, professional, and objective assessments of the potential viability effects of various alternatives, not necessarily to champion any one particular alternative. The viability risk assessments should make it clear which alternatives provide well for viability and which do not.

To help the viability committee become a working partner with the planning process, it seems to me that the committee needs to be formally recognized and sanctioned by each participating agency, and that their time be officially allocated to refining their draft conservation strategy guidelines. I would envision that the committee would then work closely and iteratively with the LMP

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team to conduct GIS analyses, to help produce alternative forms of the conservation approach, and to advise LMP in interpreting the assessments.

Specifically, access to GIS and to the forest inventory data are needed so that the viability committee can assist the LMP to better fit the conservation strategy guidelines to unsuited TM lands, wildernesses, LUD II lands, and other set-asides, to reduce impact of habitat conservation on the timber base. As I understand, the current habitat conservation map is but one possible "solution" to applying the standards and guidelines. Other, possibly less timber-costly, solutions are possible; but the LMP must work closely with the viability committee to ensure correct application of the guidelines for designing alternatives, adherence to the principles and intent of the guidelines, and correct biological interpretation of the results.

The viability committee is interagency; this can be promoted as a very positive coordination among agencies -- particularly USDA Forest Service, USDI Fish and Wildlife Service, and Alaska Department of Fish and Game -- and other interests in southeast Alaska. USFWS and ADFG -- at least the biologists involved in the project -- seem to have been a very helpful and willing participant on this particular viability committee. Not to sound cynical, this is a too-rare treat when two federal and one state agency can work so well together on such a task. In conservation planning for the northern spotted owl, we have used several similar interagency technical groups to help oversee application of planning standards and to interpret new scientific information.

As with planning for spotted owls, grizzly bears, and other wildlife, higher-level line-authority teams also have proven helpful for interagency coordination and delegation of duties to the technical committees. Such line-authority groups include the Interagency Grizzly Bear Committee and the Interagency Northern Spotted Owl Conservation Group, and they have worked successfully elsewhere. Tongass NF might propose the formation of such a group and participating in it to help resolve any fish and wildlife conservation concerns.

5. Wildlife species conservation planning is best done to avoid T&E listing. Why do all this work now, if we are not dealing with threatened or endangered species? I cannot stress this point strongly enough: The best use of wildlife species conservation planning and viability assessments is to prevent currently secure species from becoming viability concerns in the future. More important, if there are species currently of growing potential concern, as initial analyses suggest (especially the scarcer species associated with old forests in southeast Alaska), then adequate preemptive conservation actions would stave off future listing. The current conservation strategy and the viability committee provide a great step ahead in such preemptive planning.

6. Wildlife species conservation planning is an important component of ecosystem management. Ensuring viable, well-distributed wildlife populations

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throughout the region is one important aspect of managing for biodiversity and ensuring a healthy ecosystem. The conservation planning approach can be promoted and marketed as one vital aspect of ecosystem and biodiversity management.

7. Seek peer review. The draft conservation strategy is a very good "first cut." It -- and its inclusion into the LMP process -- could greatly benefit from additional technical peer review. We discussed the possibility of enlisting the aid of other Forest Service researchers and specialists in species conservation. I would suggest that a second draft of the strategy document could be crafted based on my and others' review comments. Then, it could be sent for review by conservation biologists and species specialists outside the Forest Service. Technical soundness and academic and biological credibility are very important to ensuring a sound evaluation and species planning process. You might consider using a semi-blind review such as used by Jack Ward Thomas during the northern spotted owl ISC process. Jack sent the draft ISC strategy to the presidents of several leading professional and scientific societies, and let the presidents select the best technical specialist to do a peer review.

Wildlife Conservation Planning On Tongass National Forest -- Observations And Suggestions

1. Background

On 18 and 19 June 1992, I visited Tongass National Forest, Juneau, Alaska, on a functional assistance trip regarding wildlife conservation strategies for the forest's Land Management Plan (LMP). The purpose of the trip was to informally review the current state of planning for wildlife species conservation, to study a proposed wildlife species viability conservation strategy developed by an interagency committee of wildlife biologists, and to provide an internal-agency peer review of these planning and conservation strategy efforts.

I met with Fish and Wildlife Staff Director John (Jack) C. Capp, and with wildlife biologists Lowell Suring and Chris Iverson. I studied and reviewed the draft conservation strategy and also spent two mornings discussing the conservation strategy with the interagency biologist team who wrote it. The team I met with consisted of biologists from USDA Forest Service Tongass National Forest, Alaska Department of Fish and Game, and USDI Fish and Wildlife Service.

I also spent an afternoon with the LMP team of Tongass NF, particularly reviewing the geographic information system (GIS) information and analyses conducted thus far on the plan. During that meeting I suggested some additional evaluations for wildlife species conservation that the team could conduct with existing expertise and information, in coordination with the Tongass NF FWL

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specialists and the interagency biologist viability committee. I will repeat some of those suggestions in this report.

My own expertise in forest planning, wildlife ecology, and population viability analysis seemed appropriate to this review task. I have worked on viability planning issues for the northern spotted owl, California spotted owl, Mexican spotted owl, Mt. Graham red squirrel, red-cockaded woodpecker, and other species, since 1985. I've been the lead scientist on two major EIS's on the northern spotted owl, developing and implementing procedures for assessing population viability. My work also includes participation on the Interagency Scientific Committee on the Northern Spotted Owl, and on the Scientific Panel on Late Successional Forest Ecosystems (known as the "Gang of Four"). I've also provided consultation assistance to the Northern Spotted Owl Recovery Team of USDI Fish and Wildlife Service, red-cockaded woodpecker evaluation teams in southeast U.S., Mt. Graham red squirrel evaluation teams of southwest U.S., and other similar projects.

I have worked in the USDA Forest Service's Wildlife-Habitat Relationships Program since its California inception in the late 1970's. I have published several dozen scientific papers and a recent textbook (another two texts are in preparation) on these and related topics. At present I am Technical Coordinator for the Spotted Owl Research, Development, and Application Program for PNW Station, Portland OR. Past positions include Area Wildlife Ecologist for Mt. Hood and Gifford Pinchot National Forests, and wildlife ecologist and biologist at district, supervisor's, and regional offices on various National Forests in Regions 5 and 6. Much of that work has dealt with population viability analysis and planning, ecosystem management concepts, and wildlife-habitat relationships. I also have international experience in forestry, forest wildlife ecology, and forest management in India, central America, the Caribbean, and elsewhere.

Overall, I was very impressed with the skills of the LMP and FWL staffs on Tongass NF and with the available technologies, including geographic information systems. The LMP team has done a fine job compiling and analyzing many data layers over such a vast area.

I am not an expert in the distribution and specific ecology of wildlife in southeast Alaska. However, there are some general concepts and considerations of providing for viable, well-distributed wildlife populations that the LMP team on Tongass NF might find useful to consider as they proceed with their efforts. I offer these comments as friendly food for thought from my own experiences in Regions 5 and 6.

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The proposed wildlife population viability conservation strategy and committee

Use the committee as a resource. I would suggest that LMP can tap into the viability committee -- if the committee is given formal recognition, sanction, and time to continue its work -- as a most valuable resource. The committee can advise on viability assessments, can help produce alternatives for analysis, and can help interpret results of evaluating effects on species of concern from short- and long-term implementation of each alternative.

Inventory, monitoring, and research

Need basic data. I was struck by the dearth of basic field information on presence, distribution, abundance, trend, and habitat associations of most wildlife species of potential concern in southeast Alaska. The proposed wildlife species conservation strategy can help retain conservation options over the short run -- as in the life of the next planning cycle -- while such basic information is gathered in an integrated inventory, monitoring, and research program.

Inventory. Inventory activities can include basic field surveys conducted in a scientific manner to describe presence, distribution, and ecology of selected wildlife species and taxa. Inventory of vegetation conditions (structure and composition) can also help in building and using more accurate models of wildlife habitat suitability. I further discuss vegetation inventories below.

Monitoring. Monitoring can take three forms, as used at least in Region 6: implementation, effectiveness, and validation. Implementation monitoring helps track how well we are actually fulfilling the standards and guidelines on the ground, once instituted in the plan. Effectiveness monitoring tests if vegetation and wildlife respond to our guidelines as we think they should. And validation monitoring tests the underlying assumptions and helps us understand why vegetation and wildlife populations respond as they do. Validation monitoring is important for providing information on what aspects of planning standards and guidelines, if any, to change over time to better meet the management objectives. Thus, implementation monitoring tells how well we are following directives; effectiveness monitoring tells what the response is; and validation monitoring tells what caused that response and what can be changed in the directives to elicit a desired response. Collectively, these 3 components form the basis for adaptive management.

Monitoring objectives should derive directly from identifying knowledge gaps and information needs, and from listing key assumptions, in the conservation strategy. Monitoring objectives should be expressed as falsifiable null hypotheses. This would help facilitate developing concise scientific study designs.

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Research. Research enters the picture mostly for validation monitoring, and somewhat for effectiveness monitoring, activities. Also, research can assist in designing good inventories of wildlife and habitats. I suggest that we pursue development of an integrated inventory, monitoring, and research program in conjunction with the FWL staff of the Tongass NF, perhaps the LMP staff, the viability committee, and the Forest Service PNW Research Lab. I would be happy to help in initial discussions to identify needs, write out objectives, sketch out a time line of activities, identify how to take advantage of ongoing management and research activities in these areas, and discuss practicality of such projects. The viability committee can assist initially in this effort by writing out its major assumptions used in its conservation strategy.

Data in the GIS

Validation of the vegetation layers in GIS. The validity of using timber type data to infer old-growth conditions and wildlife habitat presence and quality really needs to be tested and quantified. Our publics in Region 6 are becoming very astute in compiling, interpreting, and analyzing remote sensing data. They often know the right (and difficult) questions to ask about data accuracy, reliability, and validity. I was told by the LMP GIS expert on Tongass NF that the vegetation (timber type) data has not been field-verified or validated, particularly as used to infer wildlife habitat suitability. This might be an important area for monitoring. Better, it might be more useful over the longer term to institute a multi-resource inventory method for general vegetation conditions (structure and composition), and from that information infer specific resource conditions.

I point out these ideas because they are potential areas of contention from public and outside reviewers of any draft plan on which these data are based. In some cases, the "best available information" might not be good enough to infer specific forest conditions for some wildlife species or to project future effects of current conditions and proposed actions. This might be true particularly when we are trying to depict more subtle forest structures than are allowed with the current crude groupings of timber stocking classes, especially with old-growth forest components in younger stands. A need for an inventory to be based on vegetation composition rather than just timber stocking classes will become increasingly important as we attempt new silvicultural methods to provide older forest components within young forest stands.

Review Comments Of *A Proposed Strategy For Maintaining Well-distributed, Viable Populations Of Wildlife Associated With Old-growth Forests In Southeast Alaska* By Suring *et al.*

On 18 and 19 June 1992, I reviewed the draft conservation strategy and discussed it with the interagency biologist team (the "viability committee") who

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wrote it. The team I met with consisted of biologists from USDA Forest Service Tongass National Forest, Alaska Department of Fish and Game, and USDI Fish and Wildlife Service. This document provides peer review comments on the draft report *A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-Growth Forests in Southeast Alaska* by L. H. Suring *et al.* (April 1992 Review Draft).

Overall, I support the viability assessment process that the "viability committee" has developed. I am very impressed by the amount of quality work the committee has accomplished with the limited resources and time available.

Is the viability strategy "right?"

It is my professional opinion that the process and basis for the proposed conservation strategy is scientifically sound, given our current knowledge base on these species in southeast Alaska. I stress "current knowledge" because we seem to lack much basic empirical data on wildlife in southeast Alaska. Specifically, we need information on habitat use and selection, and potential utility of alternative silvicultural practices that could be designed to maintain components of old forest habitats.

There is an embarrassing dearth of basic field information on species presence, distribution, and density, as well as on historic and current trends of populations and habitats, and population demographic dynamics. Much needs to be learned on all of these topics. The strategy can help retain conservation options over the short run (e.g., the life of the next planning cycle) while basic natural history studies can be instituted.

The viability assessments, along with some of the mapping activities I describe below, can be useful for initially identifying key taxa and geographic areas of potential concern for which inventory and monitoring studies can be made high priority. Such studies would help us identify how to amend the conservation strategy to better provide for wildlife species and human resource needs concomitantly. But for now, the viability assessment strategy could be thought of as an interim measure for maintaining viability options and opportunities over the short run, and as a set of management hypotheses to be tested and validated through scientific field surveys and studies.

Definition of well distributed

Based on my experience with viability planning for spotted owls and other species, I might suggest a clear, ecologically based, working definition of "well-distributed." Two main principles of well-distributed are connectivity and variation.

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A well distributed population is one that occurs throughout at least its current geographic range, and possibly one that is restored in portions or all of its historic range, such that individuals are able to interact throughout the population. Thus, maintaining or restoring connectivity among populations that have become fully or partially isolated from management activities is a key to providing well-distributed patterns.

Also key to the concept is maintaining species distribution among the full range of environmental conditions over which it presently occurs or historically occurred. Maintaining such variability of environments throughout a species' range is vital for long-term selection and adaptation. This is particularly true at the edges of a species' range, which are sometimes discounted as not needed for conservation. The edges or margins of a species' range often provide unique environmental conditions where ecological and evolutionary dynamics might occur, such as character displacement and development of new subspecies, species, and evolutionary stocks. Maintaining the full environmental range is also particularly important in maintaining population persistence in light of global changes and shifts in regional climates.

In a setting of archipelagoes and true islands, it would also be important to maintain the variation in environmental and ecological conditions among subpopulations found on different islands and habitats. Conserving diversity among populations and subpopulations is key to maintaining genetic variation and options for future adaptation. I suspect that the island complex of southeast Alaska is rife with ecotypes and locally adapted forms of many species, particularly small-bodied, less vagile species. Again, much basic inventory and taxonomic work remains to be done to describe the biological heritage within the forest. The glacial refugia of southern southeast Alaska could be an obvious place to begin such work.

General comments on viability analysis and planning

Document evidence of change. It might be useful to document any direct evidence of population declines in disturbed areas, particularly over the past several recent decades. If such information is not available, then it might be useful to (a) characterize from available field studies the macrohabitat conditions with which each wildlife species considered is closely associated, and (b) display the historic and current trends in amount and distribution of such habitats. If such information is unavailable for the entirety of the species' range within southeast Alaska, then representative areas can be depicted. The idea is to display and hopefully quantify the rate of change in overall population size, extent, or habitat conditions.

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A given species might still be a viability concern even if it has not displayed recent declines in abundance or distribution. This is the case if the species has particular life history characteristics that make it vulnerable to impending or potential changes in its habitats or environment. The life history and other criteria that the viability committee used for screening potential viability concern is a good list and is what I am referring to here.

Depict areas of concern. Closely tied to the above task would be to depict what might be called "areas of concern" of existing conditions for each species, and the potential vulnerability of such areas.

I would follow a 3-step process for this. First, create a map overlay for the region -- one overlay for each species -- delineating the following categories of areas of concern:

- critical links ("pinch-points") in habitat and population distribution; these include geographic bottlenecks and cut-points in the species' distribution within southeast Alaska

- known or suspected dispersal barriers (remember, one species' barrier might be another's corridor)

- areas with low crude population density (low because of natural conditions, such as presence of muskeg, because of past forest management activities, such as clear-cutting, or because of other factors such as human habitations)

- known or suspected population isolates (for small-size terrestrial species with poor over-water dispersal capability, this might include many individual islands; denote each as an isolate)

- historic range of the species in which it is now extinct (for whatever natural or human-caused reasons)

These overlays are powerful communication and education tools. They readily depict much information on where species are more secure and more vulnerable, at a glance.

In the GIS, one can overlay these maps among all species of potential concern and thereby generate a composite "gap analysis" of the major areas of concern among species. I suspect that many islands and some areas heavily harvested in the past might show through all species' layers as a common area of concern. The point is not to discount areas of concern of just one or a few species, however, but rather to depict the full union of all areas of concern.

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Second, I would then overlay these maps of areas of concern with a layer depicting proposed forest management activities over the next 10, or the next 150, years. This should result in a map composite highlighting which areas of concern are particularly vulnerable in the short and long term by proposed forest management activities. This can be done for each proposed planning alternative, if they differ in mapped activity areas.

Third, I would then overlay the map depicting the one possible solution of the viability conservation strategy guidelines, showing Habitat Conservation Areas (HCAs) type 1 and 2. This overlay composite would be useful for showing which areas of concern, and which areas with additional concerns from proposed forest management activities, would be alleviated by instituting a habitat conservation area there. It would also highlight potential areas of concern that would not be covered by a proposed HCA. (It might also be useful for identifying areas where alternative silvicultural methods might be tried, and where inventory of wildlife and habitat are high priority.)

The purpose of this 3-step process is to provide information that is complementary to the draft conservation strategy to ensure that key areas have been addressed.

Additional screening for species of concern. In general, the parameters used to screen species for potential viability concern were good ones. A few were somewhat ambiguous. You also might consider using one or two other screening methods to see if the same species recur in the priority list.

One can use the modification I made of the Rabinowitz *et al.* rarity rating chart, or the chart on level of protection table depicting viability rating by Schonewald-Cox. Both of these species "filtering" methods are depicted in the paper on viability assessment, enclosed (Marcot and Salwasser, 1991:7-9; see also p. 10 for an example of using the rarity rating chart).

The aim here is not to dispute the results of your filtering process. Rather, it might be useful to see if other species filter out as potential viability concerns if a different set of criteria were to be used. With the viability committee's intimate knowledge of the species present in se AK, I suspect that an additional filtering process could be done in rather short order.

Discuss silvicultural options and information needs. The conservation strategy -- or the Tongass NF land management plan -- can discuss the potential use of silvicultural options and opportunities for meeting species habitat needs. This was not discussed very fully in the draft conservation report. Along with silvicultural options should be a discussion and listing of information needs for helping develop such options. Information needed, for example, for the northern spotted owl includes: (1) clear descriptions of forest habitat structure and composition in a form usable by a silviculturist to develop site-specific

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prescriptions to create (restore) or maintain such conditions; (2) evidence of vegetation response (structure and composition) to application of specific silvicultural prescriptions other than clear-cutting; and (3) evidence of spotted owl population response to vegetation conditions resulting from silvicultural activities. Other needs include a tracking system to follow prescriptions and responses over time.

Explain how the conservation guidelines were derived. The method by which individual species' ecologies and habitat requirements were described and then combined into the overall strategy was not well described in the draft conservation report. This needs further explanation. The process and specific numbers should be trackable from start to finish and repeatable.

In laying this out, it would be useful to also articulate the key assumptions underlying this approach and to cite similar approaches taken elsewhere. One key assumption is that of the "most restrictive" approach; that is, the habitat area and spacing needed to provide for those species with the largest use areas or shortest (mean? modal?) dispersal distances are assumed to also meet the needs of all other species with smaller use areas and longer dispersal distances. Another assumption is that the same area of ground would be used concurrently by more than one (all?) species of concern.

The viability risk ratings should also include results from mapping each species' distribution, as suggested above.

Depict impacts incrementally. It has been my experience in working with planning for management indicator species and sensitive species, particularly with MR's (management requirements) for pileated woodpecker, marten, and spotted owl, that impacts of imposing a wildlife conservation standard can be depicted in several ways. One assessment might show the total land within conservation areas that could otherwise be usable for timber production. Another assessment might show the incremental subtraction from the timber base from conservation areas after all other land allocations are made. The first approach might drastically overestimate the impact of any one land allocation, such as for wildlife conservation, on timber production. It seems to me that the second approach is a more reasonable representation of impacts on suitable timber land and ASQ.

Include modeling as a next phase. Aside from the need for basic field information on distribution, abundance, and habitat associations of many wildlife species, I would also include the building and use of demographic and habitat-relationships simulation models as a phase of validation monitoring. The habitat suitability models used in the LMP analyses should be thoroughly documented, peer reviewed, and published, if they have not already been through this process. Beyond that, it is of use to develop and evaluate stochastic simulation models to assess dynamics of demography, environmental

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conditions, and habitat. Such models, as used with the California spotted owl, have proven helpful for generating hypotheses on population trends and habitat associations, for identifying key demographic parameters of research interest, and for posing management hypotheses of areas of concern (areas of low connectivity, dispersal, and occupancy rates over time). Building and using simulation models can be done in concert with field studies of species and habitat relationships.

Gear the viability goals to population generation time. As a rule of thumb, providing for viable, well-distributed populations over 100 years is a good time frame. To be more biologically precise, the time frame might be scaled to the demographic generation time of each species of interest. The objective would be to provide for viable, well-distributed populations for at least 10 generations. I picked 10 generations subjectively; it's a span of time that, if a population is going to show a demographic decline or adverse short-term genetic effects such as from inbreeding or genetic drift, it would likely do so over that duration.

Obviously, species that are long-lived and late to mature have longer generation times, and would require a longer absolute time frame for this viability objective.

Revisit the viability rating for marbled murrelet. You might want to revisit the viability rating you gave to marbled murrelet, and think about beginning some basic surveys for presence in forest habitats on the forest. I've asked FWL R-6 to send to the FWL Unit of Tongass NF the current protocol for conducting surveys for the species within forests.

Specific comments on the draft report

Here are a few key points:

p. 5 -- Could be useful to present a few summary statistics on forest distribution among the islands, and some statistics on island size and spacing. Much of the conservation strategy is founded on viability concepts that distribution is of key importance, and that the true oceanic islands of southeast Alaska might be isolating some species. Supporting descriptive information on such distribution effects would be helpful. Also, present such information on the "distribution" part of the viability equation; the "numbers" part of the equation seems to have been well summarized by the LMP team's data analyses.

p. 5ff. -- Be sure that "old-growth" is clearly defined, and that it is clearly related to our understanding of wildlife species' habitat selection on the Tongass NF. For example, in the middle of p. 6 there is reference to 10 types of old-growth on Tongass NF. Are all 10 types used and selected by the wildlife species of interested? This is unclear.

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p. 12 -- Be careful not to assume a decision-making authority in this conservation strategy. Of course, any specialist would like to see "their" resource be managed "risk free" as you state. Line level decision makers, however, must balance many forms of risk (viability, economic, political, etc.) for multiple use. Can management ever be truly risk free? Keep your strategy descriptive and assess viability risks of potential conservation approaches. Let the line authorities decide and prescribe.

p. 14 -- Much of the process by which the sizing and spacing of HCAs, and the need for HCAs over other silvicultural-active approaches, are not well described. Specifically on p. 14, for example, what is the regression equation referred to? The citation is "USDA Forest Service, unpubl. data." Present the data and analysis here. In fact, I'd be cautious about all the citations to gray literature that permeate the manuscript (e.g., bottom p. 31); refer more to primary, published work.

p. 21 -- Also explain why corridors per se are better than managing the forest matrix for old forest components. Here are a few questions I've asked on use of corridors in other conservation projects:

- What evidence is there for the species of interest that they would use corridors?
- What is the intended purpose of the corridors: to provide primary reproductive habitat, to allow movement of animals, to connect demes genetically isolated by distance, or some other purpose?
- Then, how does each corridor network function for each species, and what is the evidence or rationale?
- What risk is there for loss of corridor forests over time from natural and catastrophic disturbance events?

p. 24 -- I don't understand how a committee of biologists "should identify their best estimate of the pair's home range." There is a hierarchy of information that should be brought to bear here: (1) use empirical data from radio-telemetry studies of pair home ranges on site; (2) if that's not available, base your estimates on population density in the area (remember, density is <u>not</u> interchangeable; or a simple inverse of, home range or territory size); (3) if that's not available, go to the literature on home range, territory size, or density of the species in another, hopefully similar geographic area; (4) if that's not available, use data from a closely related species. I wouldn't just "estimate" home range from some best-guess method.

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p. 30 -- Need a map that shows all suitable habitat distribution within wilderness and LUD-II boundaries, to offset the impression that there's so much habitat already set aside. Also helps display potential distribution risks.

p. 46, Table 1 -- Many of these criteria are ambiguous or vague. Really need full text descriptions of how each was interpreted and used. Need definitions, for example, for terms in Table 1 including essential, limited, relatively, down, etc.

Minor point: Tables 1, 2, and others refer to species and subspecies as well.

p. 48-49 -- This ranking scheme is a good procedure. Be sure it's fully described and repeatable. Conclude each species' appendix with a table (same format for each species) showing how its attributes were summarized and used in the ranking process, and what the ranks are.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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1. Background

My view of forest planning on national forest lands can be stated in two principles. First, forests should be managed in an ecologically sound and sustainable way. Second, forests are public property and should be managed for the public good. That good includes timber products, watershed protection, preservation of biological diversity, recreation, aesthetics, and sound public policy with reference to local economies. In my estimation, the Tongass National Forest has failed in the past on both counts. I realize that the agency is buffeted by pressures from the timber industry, local communities, and directives from Congress. But it is also true that the agencies' internal hierarchy and ethos has favored timber products over all other values. No matter what the equitable distribution of culpability, the Tongass National Forest has failed the public interest. Hopefully planning documents such as this one will rectify this situation.

Consider the issue of ecological soundness of timber harvest on the Tongass. All other values aside, timber harvest should be conducted on a scale, and by means that mimic the natural processes of the unlogged forest as nearly as is feasible. This is not because of some mystical wisdom of nature, a la John Muir. It is because of the pragmatic fact that the natural pattern is the result of a long history of natural selection of the plants (including commercially valuable trees) and animals that encompass their trophic, competitive and other interweaving under the regimes of climate and geology. We know this system works. We know it is sustainable. Any other system is an experiment. When applied to 17 million acres it is an incredible gamble of the public wealth.

The natural forest process of the Tongass is a small patch (some knowledgeable individuals say single tree: windfall is a problem associated almost entirely with clear-cut logging), shifting mosaic. Aggregations grow old, die and are blown down. Only a small proportion of the total forest is affected at one time. This would dictate that timber harvesting be conducted by selective cutting or in small patches among the more mature stands. The Tongass is being

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logged in thousand-acre clear-cuts. This system has some rationale in the redwood and Douglas-fir forests of California, Oregon and Washington where massive fires produced even-aged stands of shade-intolerant species (although no one has explained to me why stands ranging in age from a few hundred to about 800 years had to all be removed in about 60 years). And in the lower states the size of clear-cuts is seldom over 100 acres on Forest Service lands.

If none of these conditions hold for the Tongass, why are large clear-cuts being used? I asked my colleagues who are silviculturists and forest managers (none of whom are fond of spotted owl-driven forest management) if there was some technical reason why this was so. They assured me that there were no technical reasons why this needed to be done. Small block removal was readily possible, and Louisiana Pacific (hardly a model of land stewardship) was even doing selective-cutting with high lead cable methods. The reason for large clear-cuts was simply engineering efficiency. They also allowed that there was widespread disapproval among silviculturists of the harvest methods on the Tongass.

Given the public uproar about below-cost sales, there is certainly merit in being concerned about cost-effectiveness. But not cutting at all is an alternative to solve economically inviable sales. It does not follow logically that ecological costs that don't show up on the ledgers should be incurred to lower economic costs.

This brings me to my second principle: public good as expressed by sound public policy. The Tongass National Forest is public land containing public resources and services. By birth as a U.S. citizen I hold (approximately) a 230 millionth share. I submit that the mill owner in Juneau, the mayor in Haynes, and the logger in Sitka hold exactly the same share. No more, no less. By proximity they may have advantage of access, but they have no special claim to the values contained in the national forest. They don't owe me a living, nor do I owe them a living.

If any individual seeks personal (or corporate stock holder) profit from public lands, then that profit should be matched (at minimum) or exceeded by public good. Clearly it is an impossible task to state the public good precisely given that timber supply-demand and price, preservation of biological diversity, national economic status, local community stability, ecosystem stability, and so on, all go into that determination. But it can be stated what is not in the public interest, such as the following:

1. It is not in the public interest to foster environmental degradation.

2. It is not in the public interest to lose biodiversity.

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3. It is not in the public interest to give windfall profits to the few at the expense of the many.

4. It is not in the public interest to create boom-bust local economies.

5. It is not in the public interest to liquidate steady-state resources for short-term gain.

Perhaps private lands cannot be managed for ecological sustainability and long-term economic planning because of the danger of hostile takeovers. All the more reason for the public lands to be managed on that basis. Indeed, that is the reason for the creation of the Forest Service in the first place.

The Tongass National Forest has a history of not protecting the public interest. It has not protected the public interest with regard to timber, much less other goods and services. I was not asked to review the forest management plan which drives the character of the wildlife habitat plan. Yet, this is the backdrop against which the wildlife habitat documents under review were drafted. They are constrained in ways that I cannot accept as sound, even though my review must of necessity be confined to what has been written. No document can be reviewed without first knowing "what are the goals of the program?" Not for a moment do I accept that minimizing the impact on timber harvest is the proper goal for a plan to preserve biological diversity on national forest lands. The goal should be preserving biological diversity independent of timber harvest which might be totally constrained or constrained not at all. There has been much rhetoric in the Forest Service in recent years about ecosystem management, sustainability, preserving biodiversity, new initiatives, and new forestry. But then, that is the lip service and this is the Forest Service.

In evaluating these wildlife habitat documents I relied mainly on four things: 1) basic principles of ecology and evolution, which underlie all biological systems and processes; 2) quality of the database that informs the planning; 3) similarities with comparable planning exercises elsewhere; and 4) common sense. Most of these are self-evident, but (2), the quality of data, needs to be examined further because of some statements in the reports with which I cannot agree.

The difference between data for management decisions and data for science is a matter of degree, not kind. Science is not "certain", it is probabilistic. It simply calls for a high standard of "proof". Because of the size of the problems and lack of funding it is certainly true that most data for management cannot meet the scientific standard, say significant at $P = 0.05$. But this does not mean that management data should not be expressed in the same terms, but at a lower threshold of acceptance, e.g., $P = 0.25$ or some similar value. To not express the error at all leads to a false sense of security that the mean values are reliable. These documents often do that. After stating that the data are weak, the

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documents often proceed to discuss and incorporate the values as if they were correct. A disclaimer is not sufficient. Low confidence must be carried through in the analysis and thinking so that the outcome is properly weighted.

Science has rigor because scientists demand it of themselves and their colleagues. It is not imposed by outside bodies. I suggest that managers need to demand high standards of themselves because it is not good enough to simply say that it cannot be done. It must be kept in mind that the consequences of being wrong, when applied to 17 million acres, are far more drastic than the erroneous paper that makes its way into the scientific literature. The degree of uncertainty must be built into the decision process; i.e., decisions must be conservative when the results are questionable, and the consequences of being wrong are grave.

I would advocate that standards for monitoring be high. If the data upon which a HSI model is built are poor, then the predictions of that model will be weak. Correcting errors can only happen if they are discovered in time to make the required adjustments. It follows, therefore, that the monitoring system be carefully designed, the parameters to be measured selected carefully, and the data meet a high standard, either equal to that of science, or clearly rationalized why a low standard will, in fact, suffice. Certainly the probability values should be expressed overtly.

2. Comprehensive Review

These documents are the result of a tremendous effort by a large number of dedicated people. The task is gargantuan. First, the Tongass forest is huge and diverse. Second, the things that should be known to do this job are immense. The approach taken is laudable. The various teams have worked diligently to bring to bear the knowledge available, and to attempt to fill in the remainder with iterative sessions of expert judgement.

Although the gaps in knowledge are huge, there are some areas that are supported by excellent research studies published in the peer-reviewed literature. These are as strong as studies done anywhere and they serve as linchpins that support extrapolation into the unknown. Similarly, there are excellent people involved in the effort. Some are well-known and respected scientists in their own right. I respect the effort that these documents represent, and I do not criticize lightly. This may be the appropriate plan if my objections can be answered convincingly.

Many of my responses are simply questions. Why this instead of that? Because we have a final document without a record of choices along the way, it is hard to evaluate fairly. Did the working team consider this approach and reject it for very good reasons, or did they fail to think of it at all?

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For example, consider the selection of species as "species of concern" (SOC) or "management indicator species" (MIS). We know the number of candidates was winnowed down over time, and we pretty well know why the species remaining were selected. But we don't know why other species were rejected. For example, why were economically important species such as the black bear, wolverine, or moose not included in the MIS list? Or why weren't the marbled murrelet (a category 2 candidate for listing by the state of Alaska) and the frog noted to be a T&E species not included in the SOC list? On a larger scale, was the listing biased by the background and expertise of the listers? Were specific efforts made to include in the discussion typically underrepresented groups (e.g., insectivores, bats, small rodents, herps)?

Another problem is the lack of verification of HSI models on given species. HSI models have many failings, as the authors clearly point out. I reluctantly agree that the field probably does not have anything better to put in place on this scale at this time, under these circumstances. The authors hardly can be faulted for these problems. On the other hand, the authors surely need to address a logical conundrum with what they propose for verification of the HSI plans.

HSI models address potential population size given the quality of the habitat, not the actual populations. The actual populations may at times achieve this level, but ordinarily would be lower because of predators, hard weather, competitors, diseases, hunting, etc., etc. Thus, the actual population over a broad area would almost invariably be below that predicted by the HSI model. The documents say that the HSI model population predictions will be compared with the actual populations in test areas to see if they agree. But, they shouldn't agree. The HSI populations should be somewhat more than the measured populations. In the black-tailed deer test, agreement was taken as verifying the model. If the parameters of the model are adjusted to bring the model predictions down to match the actual population, then the model is no longer an HSI model, the logic of HSI approaches is subverted, and the model, in reality, is attempting to predict actual population size. Conversely, if the authors accept that actual population should be lower than HSI predictions, how much lower should it be? Clearly if the observed population is greater than the HSI prediction, the model is wrong. But if it is lower, how does one determine if it is the right amount low? What are the criteria for deciding a value "verifies" a model and what are values that would "unverify" the model? Even if the species goes to extinction it does not necessarily mean that the habitat was not suitable, even of high quality. Many large mammals were extirpated from excellent habitat in past history.

I would argue that there is no logical way to verify an HSI model. It is an expert judgement system about habitat quality that lacks an objectively measurable population size correlate that will verify the model. It proceeds from "we think this is right" at development, to "we still think this is right" after comparison with empirical results, which may agree or disagree greatly

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depending on the combination of other factors impinging on the population over its recent history. This is exactly why HSIs have such a poor reputation in the scientific literature. And it is why some habitat advocates' saying the population work is not necessary is short-sighted to say the least.

What should be done about verification of HSI models in the Tongass wildlife plans? I don't know. I suppose it all can be ignored and go ahead and match the predictions with the empirical results. But of course, this means that a HSI model is not really what the model is; it is a direct population predictor. Or, the HSI prediction could be retained and considered as useful if the observed population was no lower than some arbitrary percentage of the predicted population. But then what do you do to protect the viability of those species with populations too low, and for which the HSI approach is obviously failing? In any case, please note the absolutely essential requirement that monitoring be precise to make any judgement about the predictive model, whatever its character.

My final major, and by far most serious comment, involves the scale of HCAs. This plan acknowledges the predominating intellectual influence of the spotted owl plan. It would be obvious that was the case even if no mention had been made. I am a great admirer of the spotted owl plan. Thomas and colleagues produced a monumental work that will be a landmark in the history of wildlife conservation. It is the first big empirical step into wildlife conservation as it will look in the world of the future. I want to make clear that my criticism of the Tongass plan applies to the strategy as applied there, and not to the spotted owl plan.

I think the spotted owl strategy is wrong for the Tongass for two basic reasons. First, the spotted owl has a fairly unique biology, and it is not a particularly good species from which to derive a general model. The owl strategy is not appropriate for species that can't fly, or even walk very well. Second and most important, the spotted owl plan was a habitat salvage operation. The old-growth forest in the northern spotted owl range was nearly gone, and the absence of large blocks of old-growth forest because of prior fragmentation set extreme constraints on the options.

Neither is true of the Tongass. There is no spotted owl and the other raptors, including the nearest counterpart, the goshawk, are substantially different in their biology. Secondly, there are still large expanses of unfragmented old-growth, and alternatives are available.

We need to go back and recall that the field of conservation biology developed in response to a world that is being divided up and parceled out, in which habitats are fragmented, isolated, and capable of supporting only small populations. The application of conservation biology in real-world planning is welcomed because of necessity, not because it is ideal. It is welcomed, not as a carload of friends but as an ambulance when the only other prospect was a

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hearse. In our rush to employ conservation biology thinking we need to remember that the old, unfragmented world was far superior for preserving biological diversity.

We must acknowledge that we know little about the ultimate value of conservation biology as an applied field. Most of the principles are derived from logic, mathematical models and not a little salesmanship. Few natural metapopulation species occurred, and we don't know much of the detail about the population and spatial dynamics on the ones that did. Many of these were secondary successional species, and it seems doubtful that interior climax species with their very different sort of biology, will be merely the flip side of the weedy species. We have few studies of metapopulations created by habitat fragmentation of continuous populations, and curiously, one of the best-studied examples, the capercaillie grouse (Rolstad, 1991; Wegge *et al.*, 1992), is not cited in these documents. We do not have a long enough record on any metapopulation produced by fragmentation to tell if conservation biology ideas will support a species over the short-term, much less 50 to 100 years into the future.

Still, sad experience, common sense, and conservation biology tell us it is not good to reduce continuous populations (even subdivided ones) to metapopulations. Furthermore, all the weird and wonderful mathematical models used to explore metapopulation dynamics seem to agree on one thing while disagreeing on most others; a large "mainland" area is stabilizing to the system (which is a roundabout way of saying a continuous population is superior to a metapopulation) (see Gilpin and Hanski, 1991 for examples).

One of the key variables in metapopulations is dispersal rate and success, and this relates to the geometry of area and distance of patches. The area of a circle expands rapidly in relation to its radius. The area of networks with nodes (patches) expands slowly with comparable distance, and the rate declines as nodes are more widely spaced. To survive what a continuous population is reduced to, a metapopulation with fragmentation, animals must be capable of dispersal. Different species have evolved different dispersal abilities so that a configuration of reserves that will serve one subset of species will disfavor the other subsets in the array of species. These other subsets will have a hard time. All species will be presented with a new problem to which they adjust or go to extinction. Given the long generation times of vertebrates and short time for fragmentation of habitats (150 years proposed for the Tongass), we cannot reasonably expect selection for increased dispersal ability to save any species, much less the big ones like bears with generation times in the neighborhood of 6-10 years. Behavioral plasticity will be our best hope but interior species have not had a selection history for plasticity because of the stability of their preferred habitat. Also for behavioral plasticity, the big ones will have the advantage (because of much learned behavior) over the small ones that are more hardwired for behavior. We might hypothesize that the big ones will be saved by behavioral adaptability and the small ones by selection, but that proposition seems

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sufficiently shaky to doubt whether it is a good idea to count on it. Even if animals solve the behavioral problems of long range dispersal can they survive the trip? Predators are not dumb and are adept at exploiting opportunities. Corridors are a subject of considerable debate, and even their advocates will admit that we really know very little about their desirable configuration (see Noss, 1987; Simberloff *et al.*, 1992). It is clear that "one size fits all (species)" is not true (Harrison, 1992).

Even more troubling is can they survive at home? There is major concern now in California about the marbled murrelet. This concern has been with saving sufficient old-growth forest habitat for nesting. Other factors have not received much attention. But of the few nests discovered and observed, a surprising number have been destroyed by ravens and jays. Even if more than enough nesting habitat is preserved, can this slowly reproducing species survive on habitat islands in an ocean of habitat favorable to ravens, jays, etc.? We plan HCAs on the biology of top carnivores and edible herbivores, and assume that the small fry will automatically be taken care of. This seems to me a blithe assumption given that the large things eat the small things, and the altered habitat in the surrounding area favors a wide variety of predators and competitors that the interior species have avoided in the past by avoiding the edges. When edges are frequent and interiors small, predation by successional predators and competition by edge species may well outweigh the minimum requirements for suitable habitat as variables influencing survival of interior species.

All of this discussion of conservation biology theory and real-world conservation of biological diversity is in support of my opinion that the conservation strategy proposed by these documents is not the best strategy. I suggest that the proposed HCAs are too fine-grained in distribution, and that the spotted owl plan is not a good model for the Tongass National Forest. I suggest that fewer, but much larger HCAs that will support continuous populations is a better strategy, and will involve fewer long-term risks.

What are these advantages? First, it will solve many of the problems of small populations subject to local extinction. Thus, successful dispersal is not nearly so critical, and dispersers need not run a gauntlet of crossing unfavorable habitat or moving through corridors. Second, edge effects are minimized, thereby ameliorating the impact of successional species on interior species. Windthrow problems, another edge effect, will be less on few large versus many small reserves. Third, large population sizes solve most of the genetics problems. Large populations contain most of the diversity, avoid inbreeding depression and drift, and maintain the demic structure. The dispersal necessary to maintain fragmented metapopulation by recolonizing extinct patches and rescuing sink patches favors swamping of deme structure. On the Tongass, the islands may well maintain demes by being barriers or filters to dispersal, and this is not an issue (the zoogeography of the area seems to support this view). But if not, it is

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good to remember that distant outbreeding has its own consequences and favoring long distance dispersal may have unanticipated genetic consequences (Shields, 1982; Templeton *et al.*, 1986). This factor is being taken into account in conservation planning of the red-cockaded woodpecker (Stangel *et al.*, 1992). Current models suggest that species in small populations require one or two immigrants per generation to maintain diversity (Allendorf, 1983; Lacy, 1987).

In the worst case scenario, if the strategy fails, the human intrusion required to perpetuate genetic diversity is much less in the few, large HCA cases. If species don't disperse successfully, artificially moving animals between many small HCAs will be an enormous checker game. It may seem that monitoring can keep up with the problem or that budgets will be available to do all of the moving around of populations. I doubt it. Only a few moves will suffice in the few large HCA strategies. The same would be true of demographic supplementation, and discovering the problem through monitoring would be easier and less costly. No specifics have been presented about exactly how one monitors the large array of dispersed HCAs.

The charge to the habitat planning team on the Tongass states that wildlife populations should be "well-distributed" over the national forest. This does not seem to me to mean evenly distributed. One could argue that several large HCAs spotted into areas not presently protected by large wilderness and other withdrawn lands could be considered well-distributed. By placing these HCAs in conjunction with existing small restricted areas (large color map), these HCAs could be made even larger. And by placement according to island (or closely adjacent islands) to include areas separated by wide dispersal barriers, demic problems and minimal dispersal could be addressed.

Assume, for sake of discussion, that the current timber harvest constraints of small, evenly distributed HCAs proposed by the plan is applied to large HCAs. Timber harvest is reduced by about 22% by the proposed large and medium HCAs, and this plus the small HCAs should come to around 25%. While I realize that timber volume (board feet) isn't easily translated into land area, this suggests that around one-quarter of the project area could be dedicated to large HCAs with no greater impact on timber harvest. Clearly the need is in the southern islands where wilderness and withdrawn areas are small or absent.

The foregoing discussions are largely theoretical and logical arguments for a management strategy with fewer large reserves. More telling is that the forest plan (*Appendix M*) and the author's own analysis (proposed strategy) show that the current proposed strategy is not as good as a few large reserves. Both the *Appendix M* and the Conservation Strategy point to the same conclusion, although arriving there by different means. By "maximum effects analysis" the areas of great risk (p. M-15) are those ecological provinces that fall in the southern islands area (figure on p. M-12) and over projections of 150 years for plan P, these provinces having lowest values on both axes for two measures of

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risk (Figure M-18, p. M-39). This same area in Fig. 4(?) (maps following page 83) shows a progressive "whitening" (low probability of maintaining viable populations) over time, and by 150 years (2140) is all white.

It is obvious that the areas that remain black by 2140 are highly associated with large wilderness and withdrawn areas. Doesn't this suggest that small, dispersed HCAs are not as useful as fewer large HCAs (perhaps even a couple of very large reserves)?

My analysis is crude because of the short time and summary materials I had to work with. Nevertheless, I believe that both theory and the author's analysis suggest that the competing strategy of fewer large reserves in the southern islands needs to be explored. Until that option is explored, it cannot safely be concluded that the present strategy is the best one available, given equal impacts on timber harvest.

3. Species Review of the Sitka Black-tailed Deer HSI

The amount and quality of research on the black-tailed deer on the Tongass National Forest is higher than for probably any other species considered. One cannot but be impressed by this body of work, produced by a succession of outstanding biologists. It is further unusual in the amount of data that has been published in top quality, peer-reviewed journals. In many ways the Sitka black-tailed deer is a model of how research and other information should support and justify management planning. There are few unknowns about the basic biology and ecology of this (sub)species. The major problem is estimation of shifts in parameters over space and time, and these must be extrapolated from the areas and circumstances where they were directly measured.

Given the fortunate availability of good data, it is not surprising that the black-tailed deer model, in my opinion, is the strongest among species with a broad habitat distribution. In terms of the primary goal of viability of black-tailed deer over the long term, I do not have great concerns. In terms of the secondary goal of satisfying the demands of a large, deer-hunting contingent, I have more serious doubts. I also think that carrying capacity for wolves will very likely be impacted over the 150 year period.

My first set of comments is directed at issues that clearly have been considered, but not presented in enough detail for the outsider to evaluate. The use of hunting kill statistics and pellet counts to "verify" the HSI model are difficult to evaluate because no specifics on their gathering, or other than the gross outcome are presented. As an aside, I note that the logical problem of verifying an HSI model by empirical data discussed in section 2 applies, but I will treat the problem as if the goal was to obtain concurrence, as the authors seem to do.

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The strength of the verification in Table 9 depends on the error bars for the pellet group counts. I don't have Kirchoff and Kirchoff (1989) at my disposal, but the error in most pellet group counts is enormous. What was the sampling scheme and what were the sample sizes? Where did the average habitat capability for Hawk Inlet in Table 9 come from? Why is it different (32.3 versus 33.8 deer/mi^2) from the value for the total habitat given in Table 8?

I think the text must clearly state that an agreement of ratios for pellet groups and average habitat capability in no way verifies the number of deer/mi^2, only the ratio. The ratio now has a 4% difference (72 vs. 76). If error in pellet counts were introduced, how would the reliability of the ratios change? How big would the difference have to be to reject the verification?

The point of these questions is not to discredit the analysis. On the face of it the results look quite encouraging. Nevertheless, the purpose of verification is not to prove that the model is good, but rather test whether it is good. The analysis should be carried further to show whether the result is good because the model is working right, or are we are deluding ourselves because the power to reject is so low?

The sensitivity analysis results in Table 9 are interesting. The consideration should go beyond the relative importance ranking. There are two very different sets of variables here. One set determines the amount of suitable habitat. These include successional stage, elevation, overstory species, aspect, volume class, and riparian habitat. Some are fixed (elevation, aspect, and riparian), whereas the rest are variables that will shift with logging. Changing these variables causes shifts in total number of animals, but not dynamics so long as minimum viable population sizes are maintained. In many ways, these are long-term, slow processes.

Snowfall and predators, by contrast, are short-time variables, and very much influence the year-to-year dynamics of deer. Although the other variables may be expected to lower the number of deer over time, these two are likely to set up oscillations over short periods of time. That predator sensitivity is low in the ranking may be very misleading. First, a 20% reduction of deer is not insignificant. Indeed, if the crude estimation of a mule deer productivity curve I suggested (McCullough, 1987) is at all realistic, 20% reduction is nearly ICC at stability, and could not be consistently sustained in an oscillating system. Second, the fragmentation of the habitat by logging may make deer more vulnerable to predators (or hunters) because they would be concentrated in fewer appropriate wintering areas, particularly in heavy snowfall winters. Finally, snowfall and predation are not independent, and deer predation by wolves increases with snow depth (Mech *et al.*, 1971).

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I think oscillatory tendencies in the deer-wolf system will be increased under forest fragmentation, and predator-pits may well be a consequence. Certainly a 20% kill by wolves and a high human hunting kill are liable to result in over-exploitation.

I realize that these considerations go well beyond the limits of HSI models, but that is another point I wish to make. HSI models are intended for cases in which few data are available. But should the analysis be limited to HSI models in cases where a lot is known, such as for black-tailed deer? I suggest not, and that some analysis of the oscillation-inducing impacts of snowfall and predation (as well as hunting) should be incorporated in the analysis.

Other things should be considered as well. The model represents an average for the whole national forest, whereas the few snowfall data show a clear cline from deeper in the north to shallower in the south (p. L-27, Table 1). Are there patterns in snowfall over years? Many precipitation patterns thought to be random are showing up as not to be so with more detailed time-series analysis, and a better understanding of the global climate engine. Variance in winter season patterns should also be examined. For HSI models, considering winter range only and excluding summer and intermediate range makes sense. But, for more detailed analysis Klein's (1965) work long ago showed that some islands are lacking in summer range.

I realize that these topics were discussed and modeled to some extent in the analysis. I suppose that my main concern is that a deterministic model cannot adequately address factors that produce oscillatory behavior, and the mean values for a 17-million acre area masks an enormous amount of variation, only some of which is included in the HSI model.

4. Comprehensive Recommendations for the Future

4.1. Philosophical and Conceptual Considerations

I believe that fewer, larger reserves in the southern islands need to be evaluated as an alternative to the many, smaller HCAs spread more evenly over the Tongass as is the present proposal. I think the spotted owl case has inordinately influenced the approach and that the incorporation of conservation biology has been inadvertently skewed. I do not agree that accepting the minimum viable population of wildlife with the minimum reduction of timber harvest should be the goal of the program. The goals should be recast in ecologically sound and sustainable ways, and then the appropriate levels of timber harvest and wildlife habitat protection arrived at.

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4.2. Program of Research

The planning process is moving forward too fast to expect that detailed biological research can be completed in time to inform such a complex plan in such a complex environment. The argument for lesser standards and greater incorporation of expert judgment, as advocated in these documents, may be reasonable. But it is prudent to recognize that such models have weak predictive power, and that it is critical to have good monitoring as the plan is put into place to discover mistakes early while they still can be rectified.

4.3. Program of Monitoring

I recommend that research effort be concentrated on development of monitoring programs that are accurate and reliable. These should meet the standards of scientific research. They should be based on sound sampling designs, be expressed as mean and variance, and be applied on a scale appropriate to the management activities. Some schemes may be appropriate for several or many species whereas other species may require specific monitoring programs. In those inevitable cases in which the monitoring program proves inefficient, and changes are made, both old and new programs need to be conducted simultaneously until the results can be equated (unless the old scheme is totally without value). Monitoring should be sufficient to measure a 20% population change with a 0.10 probability. For T&E species or other species at critically low levels, research should be at much greater intensity than that associated with monitoring.

5. Comprehensive Recommendations for the Future for Sitka Black-tailed Deer

5.1. Philosophical and Conceptual Considerations

I think it would be useful to do modeling beyond HSI models for this species, because such modeling can be done without additional data. If the proposed HCA strategy is adopted and carried out to 2140, I think that oscillatory problems will be extreme and the hope of maintaining deer populations of sufficient size to feed wolves and satisfy deer hunters is wishful thinking. I do not think that a deterministic model can adequately evaluate these problems.

5.2. Program of Research

The need for general biological research is far greater for other species for which little is known than for deer. However, unless detailed data on the pellet

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group surveys show them to be far more successful than they have been in other regions, the need for research on an effective monitoring system is required.

5.3. Program of Monitoring

Monitoring deer in heavy cover environments has been a most difficult problem. Perhaps pellet group counts will turn out to be the best that can be done with the funds and manpower available. Aerial infrared thermoscanning with the newest generation of scanners would seem promising, and at least worth some initial trials.

6. Other Comments

None.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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USDA Forest Service

1. Background

I am not a scientist and will not approach this review from the standpoint of a scientist with particular expertise in one or more given species, nor any specific situation particular to the Tongass. In fact, I will have no comments on the habitat capability models except to say that they appear to be thoroughly constructed and the structured process for development of the models is excellent and should be completed. My expertise is more in the realm of the integration of science, technology and policy and the application of such to management problems and programs.

I am greatly encouraged with the emphasis the Forest Service is placing on ecosystem management and am personally doing everything I can to institutionalize it within the agency. I believe that ecosystem management is very simple in concept but is extremely difficult to apply especially in a multiple use environment. The concept goes back to Aldo Leopald's original thoughts of saving all the parts and pieces and allowing their interactive processes to function. The application of such a concept requires tremendous knowledge of those parts, pieces and processes - knowledge we presently do not have and probably never will fully possess. So, the train doesn't stop; people are a part of the equation and we must do the best we can to apply the knowledge we presently have, gain new knowledge and practice adaptive management along the way.

As an administrator, I have dealt with numerous technical and policy issues concerning multiple-use land management. Perhaps the greatest of these has been my staff's recent completion of a Draft Environmental Impact Statement for the Management of the Red-cockaded Woodpecker and its habitat on National Forests in the Southern Region. In spite of the single species inference in the title, this document is an excellent example of an ecological approach to restoring the ecosystems on 2 million acres of National Forest land for all of the species occurring thereon.

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2. Comprehensive Review

"Proposed Strategy"

I approached the review of "*A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska*" from the standpoint of process. I tried to place myself in the shoes of a line officer in Alaska - trying to evaluate the sufficiency of this document, along with the habitat capability models and the viability risk assessment to substantially influence or control the selection of a Tongass Land Management Plan (TLMP) alternative.

In order to have a strong wildlife and fisheries program that addresses the traditional values in wildlife and fish management for the enjoyment of the American public, as well as the conservation of the variety of native ecosystems, habitats, and species, a Forest plan must do the following:

1. Identify the components of the wildlife and fish resources that will be emphasized in planning. These components will be the management indicators.

2. Develop desired future condition (DFC) statements that have meaningful descriptions of wildlife and fish resources and habitats.

3. Develop wildlife and fish goals that describe in broad terms what a forest wants to accomplish to meet the DFC.

4. Develop specific wildlife and fish objectives that describe the specific short-term and long-term desired wildlife and fish outcomes that are needed to achieve the goals and DFC.

5. Design wildlife and fish standards and guidelines (S&G's) to move the Forest toward the DFC and to achieve the WL/F objectives.

6. Develop a wildlife and fish monitoring and evaluation program to determine the success in achieving the DFC, goals and objectives and how well the S&G's are being implemented.

Although the above points relate to the total forest planing process, I have reviewed the proposed strategy with them in mind.

I know that the proposed strategy deals only with wildlife species associated with old-growth. Since it is stated that "the vast majority of productive forest land in southeast Alaska is classified as old-growth", it may be that the proposed strategy completely identifies all components of wildlife that will be emphasized in planning. I am curious as to whether this is the situation or are

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there some of the 356 species (p. 13) occurring in SE Alaska which are not associated with old-growth and for which there may be viability concerns. If so, I assume these have been identified in the TLMP. Nevertheless, the proposed strategy seems to have provided a rigorous process to identify which old-growth associated species will be management indicators. Of course, a part of this process of selecting management indicators is to conduct a risk analysis for the species occurring in the planning area. This has been done and I will comment on the risk analysis later in this review.

The desired future condition statement for wildlife resources is a forest plan function and should include broad, forest landscape descriptions of the desired communities/habitats and the associated wildlife and plants that will be found there. The proposed strategy provides a strong basis for ONE desired future condition. The proposed network of Habitat Conservation Areas (HCAs) along with their standards and guidelines appear to be rigorously analyzed and offer one excellent solution. I cannot believe, however, that these particular lines on the map are the only solution. There must be other equally effective ones.

The emphasis in both the proposed strategy and the viability risk assessment on adaptive management as new knowledge is gained is excellent. The Region and Station should mutually decide on research priorities if this has not already been done. The TLMP should subsequently be amended as necessary to incorporate such new research information.

These three documents under review certainly provide a strong basis for the development of goals, objectives and standards and guidelines for old-growth species. In fact, standards and guidelines are presented for each of the old-growth management indicator species and these have been combined into one set of forest-wide standards and guides. Some of these standards and guides are based upon admittedly inadequate data. I'm presuming that the information is the best available. The other technical reviewers of these drafts will help determine if the best available information was used.

As a manager, I would not be comfortable with the lack of specificity in most of the individual species monitoring recommendations. Also, monitoring recommendations were not presented for several species. I understand, however, that the recommendations may be the best that can be done with the current knowledge. The technical reviewers should help determine this.

Viability Risk Assessment

The viability risk assessment very logically and clearly reviewed the species present in the planning area and properly categorized them to arrive at the management indicator species for which there may be a concern for viability.

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The three analyses of wildlife population viability were clear and easy to understand by this reviewer, with one exception - the pinch point analysis. How were the four pinch points identified? Were other possible pinch points identified and subsequently rejected? A simple documentation of the pinch point identification process would be helpful.

3. Recommendations For The Future

1. The "proposed strategy" should do either of two things. One, if the authors of the "proposed strategy" feel that the habitat conservation areas are biologically "cast in concrete," then a stronger justification should be provided. Two, if, however, there are biologically feasible alternatives to exactly where the HCM lines are drawn on the map, then that flexibility should be built into the system.

2. Strengthen the species by species monitoring techniques so that the TLMP team may use them to construct a strong, logical monitoring process for the plan.

3. Provide more documentation for the process used in the viability risk assessment pinch point analysis.

4. Further Comments

It is obvious that a tremendous amount of excellent work has gone into these three documents. Their review makes me wish I were a subject matter expert in the species involved so that I could delve into these models. But since I'm not, I must content myself with looking at processes. The documents provide an excellent basis for considering old-growth associated species viability in the Tongass Land Management planning process.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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British Columbia Ministry of Forests

1. Background

Regarding the ecology of grizzly and black bears in a managed landscape, my review is largely based on personal research and experience. Several graduate students and myself have studied the population dynamics, general ecology, and behaviour of black and grizzly bears in the Flathead drainage of B.C. for 15 years while considerable industrial activity occurred. I have also been involved with bear research projects in six other areas of B.C. and the Yukon and these have helped diversify my perception of bear ecology and management. In addition to my own work, publications and discussions with Rick Mace, Chuck Jonkel, Keith Aune in Montana, Dave Mattson in Yellowstone, Keith Simpson and Tony Hamilton in B.C., Lynn Rogers in Minnesota, and John Schoen in Alaska have greatly influenced my understanding of bear ecology and human activities.

My understanding of the principles of conservation biology is primarily based on books edited by M. Soulè, and M. Soulè and B.A. Wilcox plus various papers by J.M. Diamond.

2. Comprehensive Review

In general I found the combination of three reports to be repetitive and sometimes vague. I think they should have been condensed into one. However, after sorting through them all, I enjoyed seeing a plan of applying HCA concepts before the desperation stage of management such was the case of the spotted owl. Congratulations for this proactive move. However, I don't know that it's wise to model a conservation strategy in a relatively pristine area after a strategy that was spawned out of a desperate case. Perhaps a different philosophy, one that avoids forcing animals into small reserves, is applicable in an area such as the Tongass.

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Various Alternatives

The three sections that I was given to review mentioned several "Alternatives" such as A, B, C, D, P, Forest Plan, Maximum potential effects, and an alternative prescribed by the Interagency committee. A few of these options were partially described, but many are simply mentioned from time to time. These alternatives may be well known to Tongass managers but, without even a brief description of them, I was confused. If various options are to be mentioned they should be described in enough detail that we can at least grasp the overall management philosophy. The description should not be limited to HCA size, numbers, and distribution but how the land amongst the HCAs (matrix) will be managed.

Classifying Species and Subspecies

I found the classification systems used in the three reports complex and confusing. There are endangered, threatened, candidate categories 1, 2, 3a, 3b, 3c, Sensitive, Management Indicator species steps 1, 2 and 3, old-growth associated species, 5 species with potential viability concerns (M-16), some are on several lists, 9 old-growth associated species (S-20), 4 requiring tracts of varying size OG (S-21), and I remember several others. All of the categorized species appear to be covered with "forest wide standards and guidelines" in Chapter 4 of the Forest Plan. It is stated with little information to convince me that these guidelines are fine to ensure viability of some species but not others.

A table of where the various species and sub-species fit into this scheme may simplify the categorization.

Evaluation Criteria

It can be assumed that prior to human intrusion, all species were doing fine, or if they weren't, they were simply destined for extirpation as all species eventually are. Therefore, I would have thought that "habitats vulnerable to land management activities" should have a higher weighting factor than 4 (S-53).

Although the criteria used ended up with species that varied in body size, population densities, densities and dispersal characteristics, it may have been useful to ensure a gradient of species to capture the gradient of scale needed. Perhaps it would be worthwhile including a few plants, a fish or two, and some herps.

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The Ecology of HCAs

HCAs are obviously great to have to ensure the maintenance of biological diversity but their management and resulting value towards conservation I found fuzzy, particularly in *Appendix M*. HCAs are to be areas without timber harvest but many are already altered, and under various "alternatives" others may also be altered. It was also suggested that if the amount of old-growth (OG) was reduced below an unspecified criteria then a HCA would have no conservation value; I doubt such a threshold is true. The question "how many HCAs can be lost before a problem with viability would occur?" (M-20) is only half the question. The other half is "what is the relationship between various types and amounts of human intrusion into HCAs and the conservation effectiveness of HCAs". For example, is a HCA with 5% of the OG removed 95% as effective as a pristine HCA? How about 20% of the volume removed using partial cutting and helicopter yarding? There are many ways of removing and regenerating conifers which result in very different landscapes but these weren't discussed at all; I will return to this. I see that in the "*Strategy*" there are guidelines for management within HCAs.

Is a land management strategy with two land classes, "manage as usual" and "protected", the best? Could not a third class, let's call it a "conservation priority area", be useful where some activities such as timber harvest are permitted but with strict guidelines? Perhaps using three land classes would result in more benefits for both industry and conservation. For example, it may be preferable in some instances to have smaller HCAs in an area where there is partial cutting or extended rotations to ensure linkage between HCAs, instead of larger HCAs in a sea of even-spaced regenerating clear-cuts with a 100-year rotation and little change of interHCA movements. Was such a third land class considered?

Viability Risk Analysis

The viability risk analysis is a measure of the loss of OG combined with the loss of HCAs, which results in a index of risk. It concludes that the loss of HCAs and OG will be different under the various alternatives, the six southern provinces will be hit hardest, and the OG and HCA losses will be gradual. Because the relationship between the index of risk and true risk is not known, the analysis cannot conclude that there is a risk with any option, however, some alternatives are likely more risky than others. Because M-20 stated that "for comparative discussions purposes, we will assume that if more than 50% of the proposed HCAs are no longer suitable ... then the province would be at high risk", then you really can't conclude (M-43) that because the number of HCAs and old-growth will be reduced below 50%, the long-term risk of not maintaining viable populations is high. Fortunately, the section on sensitivity follows.

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Desired Non-Native Vertebrates

Can the maintenance of both viable populations of native and desired non-native species be the true goal or would it be better to place native species first and, if there are no potential problems, exotics second? Because we are not told which exotics are desired in the Tongass, we cannot judge the importance of maintaining these, but there are almost an infinite number of examples where desired exotics have caused the demise of "less important" native species. Of course the vectors of demise have not always been obvious.

Habitat Versus Harvest

Although all species can be greatly affected by habitat change and fragmentation, hunting, trapping, and control killing have likely impacted North American populations of wolves, bears, otter, marten, and mountain goats to a much greater degree. Some extinctions or near extinctions due to overharvest are clear and some people believe overharvest has been the driving cause of extinction in North America since the Pleistocene. A conservation plan that does not address the various forms of legal and illegal harvest is not complete.

3. Species Reviews

Brown Bears

As Table 16 in the *Strategy* shows, a lot of very good research has been done by J. Schoen, L. Beier, and K. Titus on brown bears on Admiralty and Chichagof Islands. Because the brown bear sections have been prepared by Titus and Schoen, they are done well.

The relationship between human activities and brown bears is more complex than with other species because it is much more than a habitat/fragmentation issue. The human/bear relationship is complicated by humans both attracting and displacing bears, the fact that bears can seriously harm people and their property, and because bears reproduce slowly and are found at low densities. Models developed in the lower 48 states, Canada, and the Tongass reduce the cumulative impact of a development such as timber harvest on brown bears into three components: habitat change, displacement, and mortality. In many areas, careful timber harvest and regeneration methods may result in minimal problems due to habitat change and displacement and may even improve bear habitat. A decade ago I was optimistic that with access planning we could have sustainable timber management and grizzly bears in the same area but after a decade of promoting access management, I am becoming increasingly pessimistic. Even in southern British Columbia where we have an abundance of

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roads, very few sectors of society, including the forest industry, are truly interested in access management. Thus, although there may be lots of bears today, the long-term persistence of grizzlies is questionable. Because of our inability to deal with access and increasing numbers of people in brown bear habitat, HCA or other no logging/no access reserves will likely be necessary if we are to maintaining brown bears over the long-term.

I would suggest that conservative hunting regulations be added to the list of resource management guidelines (S-172 and S-185). It also think that a PR person should be hired with a portion of timber sale receipts to promote access management and conservation concepts; if local people want it, access management is easier to fund.

Regarding the model, I would have thought that the density of bears (bears/100 km^2) in each habitat could have been simply calculated from the average density of bears in the 365 km^2 Admiralty study area (1 bear/2.6 km^2 which is 38 bears/100 km^2 or 140 bears) and the proportion of time each bear spent in each habitat. For example, from Table 3 (S-I-25) we see that 55% of the study area is upland OG or 200.75 km^2 of this habitat. The telemetry data shows that at any given time an average of 24.5% of the 140 bears or 34.4 bears will be in this habitat and thus, the average bear density in upland OG is 17.14 bears/ 100 km^2. Using this method, the average bear density in each of the eight habitats that were studied were:

Table 3:

Habitat	Average # of Bears	Area (km^2)	Density (bears/100 km^2)
Upland OG	34.4	200.8	17.1
Upland Subalpine	7.3	36.5	20.0
OG with fish	75.2	18.3	412.2
Beach fringe	2.8	11.0	25.6
Avalanche slope	7.7	18.3	42.3
Alpine	3.9	36.5	10.7
Estuary	7.4	7.3	101.9
Other	1.5	36.5	15.4
TOTAL	140.2	365.1	

Bear densities in habitats that were not in the Admiralty study area will have to be estimated using best professional judgment as was done before. These results, which should be the true densities, suggest very different relative importance of the habitats. For example, using the method in the report, O-G

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with fish would have a density of bears only 1.76 times that of avalanche chutes yet the telemetry data suggests they received about 10 times the use. If we assume that importance per km^2 is proportional to average density, then O-G with fish is four times as important as estuary and way more important than any other habitat. Although I'm not an expert when it comes to coastal bears, I would expect this to be true for the late summer (salmon) season.

So if we assume that the late summer (fish season) was the only limiting season (as stated on S-I-8) then the data presented suggests to me that O-G with fish is so dominant that the GIS model would only be sensitive to logging near fish streams. However, I don't think that the system is that simple. The low reproductive rate of Admiralty bears suggests to me that adult females may not be getting the nutrition from the fish that might be expected. First, is there a difference how the sexes and females of various status use fish streams? Second, do the sexes get equal numbers of fish? Third, could not spring be also important because this is when cubs rely mostly on lactation and therefore demands on the mother may be highest?

I don't see where reductions in habitat capability due to human activities/ disturbance (Table 5, page I-27) occur in the program code of the model. Am I missing the routines somewhere or is this a fairly serious omission?

Black Bears

There is relatively little known about black bears in the Tongass so habitat values are more subjective. However, considering the increased subjectivity, there are many more habitat classes in the black bear model. In particular, the black bear model divides riparian into 32 different classes while the brown bear model only uses two. In addition, the black bear model incorporates 3 seasons, the brown bear model only one. Why are these models so different? Is it that we know enough about brown bears to know that we don't know enough to split things too fine, whereas we know very little about black bears so can freely put numbers into many boxes?

As was the case with the brown bear model, I didn't notice the habitat capability reduction due to human activities in the code.

Both Species of Bears (and perhaps others)

Because even the largest HCAs will be much too small to ensure viability of either bear species on their own, how the land between HCAs is managed is most important. In the critical interHCA matrix, both HSI models show that changes in the output are due mostly to timber harvest and consequently, I think more effort should be put into stratifying cutting units. Cut block size is an

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obvious variable. Is a 500 ha clear-cut the same value to bears as 50, 10 ha clear-cuts? How about post-logging treatments? Are blocks that have had some veg-management (herbicides, mechanical, sheep, burned, etc.) the same as those simply cut and left to fend for themselves? How about differences between clear-cuts, shelter woods, or partial cuts? There may not be anything but clear-cuts in the Tongass but why not incorporate professional judgment on other silvicultural systems? Such speculation may suggest to the timber industry that experimenting with some other methods may be worth while and work well for industry and bears at least in some sites.

Management of the interHCA matrix is also complicated by the extremely fractured natural setting of the Tongass Forest. A land use plan of this scale must incorporate the islands, ice sheets, and fjords, not simply have HCAs of various sizes and spaced at various distances. How the HCAs are shaped and spaced in the complex environment is important.

Another note worth mentioning is that the bear models do not include competition between the two species. Competitive exclusion is suggested by a general lack of coexistence of the two species on the islands and thus it may be a significant factor in planning for the long-term conservation of each species.

4. Comprehensive Recommendations for the Future

4.1 Philosophical and Conceptual Considerations

As previously mentioned, having a "conservation priority zone" may be useful. For example, such a zone may only permit partial cutting and spot planting and be located between HCAs. Some organisms (plants, insects, amphibians, small mammals) may not be able to move through an intensively managed landscape, but may live and travel through partial cutting. I mentioned partial cutting because this silvicultural method may simulate the natural disturbance regime in a coastal system and thus species may be more adapted to it than clear-cutting. The timber industry would prefer clear-cut than partial cut, however, they would generally prefer to partial cut than to leave uncut and, they may find partial cutting better once they re-learn and re-tool.

In addition to HCA from logging, I suggest hunting/trapping reserves as well. This is for three reasons. First, overharvest has in the past been very detrimental to some species and we don't know that this is not continuing. Second, if individuals are to disperse among HCAs, they may need to approach carrying capacity before doing so and consumption may prevent this. Third, if the forest industry is going to "be stuck with the bill" for conserving species, they may resist less if others are too (We have all heard the "if they are so rare and valuable, why hunt them?" argument).

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A few final points regarding the very complex natural setting of the Tongass Forest are:

1. The HCA's size, shape and distribution plus the interHCA matrix must be distributed with the complex natural setting in mind to maximize benefits.

2. The natural setting of islands, ice, and fjords promotes fragmentation that is a doubled-edged sword. Fragmentation influences both evolution and extinction. Evolution we must encourage so island endemics must be maintained. These will likely be smaller animals with limited dispersal capabilities. Extirpation rates are increased on islands so we must ensure that human activities do not exacerbate this. These two interrelated events must be incorporated into such a plan.

4.2 Program of Research

The Alexander Archipelago may permit some unique opportunities for research on the process of fragmentation/extirpation/recolonization. True islands are no doubt better barriers than habitat islands so the significance of islands in general on species and genetic diversity in a temperate coastal system could be measured. On the mainland or larger islands, habitat fragmentation due to human activities as barriers to dispersal could be measured and then models made with the true island data as a base. Again, habitat fragmentation should not only be clear-cuts, but dispersal/occupancy of partial cuts should be looked at. The effectiveness of various buffer widths around riparian areas and different management practices within buffers should be investigated for several species.

For bears, the habitat/population models should be tested on the mainland where circumstances are quite different than on Admiralty. This work should be done in conjunction with B.C. if possible. Dispersal behaviour should be measured on both the islands and mainland. The quest for an inexpensive, extensive monitoring method should continue.

4.3 Program of Monitoring

I have no specific suggestions for ongoing monitoring except basic population monitoring of MIS and other sensitive species. Monitoring populations in an operational scale experiment and then modifying methods based on these results (adaptive management) may provide more meaningful information from a monitoring program.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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Director
Central Canadian Rockies Wolf Ecology Project

1. Background

I am the product of a Canadian mother and American father, which gives me a North American, rather than national perspective. As a 5th generation Oregonian I inherited the Utilitarian world view of my pioneering ancestors. In recent years, however, my attitudes have become increasingly more inclusive of other views. This is probably in recognition of the obvious incompatibility of our current economic paradigm and a sustainable environment.

My academic background includes a degree in philosophy with extensive instruction in environmental ethics. My ecological training has been in applied wildlife biology and behavioral ecology, with a focus on large carnivores and associated prey species. In recent years the conceptual framework of my research has been swayed by developments in sociobiology, metapopulation theory, and conservation biology. The works and writings of E.O. Wilson, R. Levin, M. Gilpin, I. Hanski, and M. Soulè have been particularly influential. My thinking about predator/prey theory and population dynamics has been strongly influenced by the combined works of G. Orions, J. Krebs, and G. Caughley. My personal environmental ethic is grounded in two principles eloquently stated by Aldo Leopold.

> "The first ethics dealt with the relation between individuals...Later accretions dealt with the relation between the individual and society...There is as yet no ethic dealing with man's relation to land and to the animals and plants which grow upon it...The extension of ethics to this third element in human environment is...an evolutionary possibility and an *ecological necessity.*" (emphasis added)

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"It is inconceivable to me that an ethical relation to land can exist without love, respect, and admiration for land, and a high regard for its value. By value, I of course mean something far broader than mere economic value; I mean value in the philosophical sense."

- Aldo Leopold, *A Sand County Almanac* 1949

I subscribe to the belief that all management decisions and recommendations must be supported by good research. In the absence of comprehensive information all management decisions should err on the side of conservatism to reflect the high level of uncertainty. However, I also believe that good science is not a substitute for an ethical framework and does not alone provide justification for any management action. Moreover, I believe we must evaluate science in the context of culture. As an example, the development of nuclear weapons is regarded as good science; however, use of these weapons is questionable.

2. Comprehensive Review

I would like to preface my comments by commending the authors for the substantial intellectual effort they have invested in developing a conservation strategy for the Tongass. Although there are several shortcomings, I am impressed with the thoroughness of some sections and the notable effort to incorporate contemporary ecological theory. Developing a management plan to address all the demands on the Tongass is an exercise in optimization using multiple variables and constraints. These types of complex nonlinear problems often have many different solutions, none of which will be fully satisfactory for all stakeholders in the Tongass. Accordingly, my comments reflect my personal biases and should be received in that context. My comments are intended to be constructive and I hope they will be used to improve the conservation strategy.

In general, the proposed conservation strategy suffers from unevenness in quality and a lack of integration. These problems can easily be addressed in revisions of the strategy. Unfortunately, structural and text revisions may be inadequate to make the strategy workable. The very laudable objectives of the strategy appear to have been compromised by a Forest Service agenda that is inherently incompatible with conservation of biological diversity. Much of the problem is related to the context in which the strategy was formulated. Two implicit assumptions dominated the conservation model that was used: environmental impoverishment and degradation are preordained; and, environmental damage can be lessened by applying management prescriptions that reflect the principles of conservation biology. Clearly, logging was given primacy over other legitimate uses of the Tongass, which means wildlife values were subordinated to extractive forestry. Several comments reinforced this perception. Apparently, the possibility of no logging was not an option that was

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considered. I am not familiar with U.S. legislation so I have to question whether this approach accurately reflects the legal mandate of the Forest Service.

Despite these limitations, any reasonable conservation strategy must address the critical problem of habitat fragmentation. Certainly the life histories of wide-ranging animals (e.g., wolves, brown bears) suggest the maintenance or restoration of connectivity in the landscape is a prudent strategy. But why design a strategy that addresses the maintenance of a disturbed environment and base it on the expectation that it will remain in a perpetually degraded condition (e.g., fragmented landscapes)? There is a clear consensus among ecologists that, all else being equal, continuous suitable habitat supports more individuals of a species than does fragmented (discontinuous) habitat. Hence, why not make the conservation goal of the Tongass the maintenance of continuous and undisturbed habitat? I suspect that the Tongass may be sufficiently unperturbed at this time to consider maintaining ecological integrity at a landscape level, without automatically defaulting to the minimalist position adapted by the current strategy.

Aside from the necessity for a non-politicized conservation model, successful implementation of the proposed management strategy is fraught with theoretical difficulties that should be examined in greater detail. A major area of concern is the process used to identify and designate movement corridors. Because success of the final strategy will inevitably depend on the maintenance of functional linkages among core reserves, I will concentrate my review on the role of movement corridors.

Conservation biology is a new discipline and many changes and controversies can be expected. For example, there are few controlled data with which to assess the conservation role of corridors, thus it is difficult to support or refute their value. There is also a dearth of information on the degree to which different species use corridors, which makes it difficult to determine if potential advantages will be accrued in each case.

As noted, the management plan assumes logging will proceed and habitats will become fragmented. Therefore, planners should consider the potential effects of occluding and rerouting established movement corridors on the long-term system dynamics of the Tongass and adjacent areas. At the very least, an effort should be made to model the development and altered dynamics of spatial heterogeneity, spatial and temporal interactions of different species, and exchanges among subpopulations across perturbed landscapes. Such an assessment will need to consider the spatial distribution and configuration of regional preservation areas; the relative distribution of critical habitats contained within the Tongass, both in and outside areas designated as protected; and the relationship of critical habitats to population densities, reproductive biology, dispersal capabilities, and connectivity. Biophysical aspects that are unique to the Tongass should also be considered in greater detail, particularly those

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landscape features that isolate populations or constrain movements. These include the heterogenous topography and archipelago structure of the Tongass.

The strategy addresses the likelihood of local extinctions in the Tongass in relation to the sizes of habitat patches (thus effective populations sizes) and the distance separating patches. This approach is valuable and instructive but somewhat incomplete. Ideally, a quantitative assessment of the risk of fragmentation requires empirical information on demographic, the condition of populations, movements, and habitat use. For most large mammals species in the Tongass, little if any such information exists. Thus, it is essential that research and monitoring be initiated to fill important knowledge shortfalls.

In the absence of these data the authors have extrapolated information from research conducted elsewhere. Such an approach may be valid but the efficacy needs to be demonstrated, especially considering the importance of decisions based on the outcome of these assessments.

The authors have also assumed that persistence-times for populations that inhabit fragmented landscapes will be greater where connectivity (e.g., via corridors) among habitats enhances the exchange of individuals (Gilpin, 1987). Certainly, much recent literature in conservation biology supports the concept of providing "corridors" of suitable habitat between populations to ensure connectivity. However the identification of existing corridors and design of corridors is far more complicated than acknowledged in the planning documents. The potential impact of impeding the "natural" movements of wildlife in the Tongass is significant because the availability and quality of alternate routes will also be diminished by human disturbances. Upsetting a movement corridor probably has effects at many scales and the zone of influence for disturbances probably varies greatly. Therefore, I suggest that rigorous guidelines be developed for designation of corridors. A number of suggestions follow: (from discussions with S. Minta and R. Noss.)

Design of Corridors

When evaluating an area's potential for conservation corridors, I believe planners should use an *a priori* analysis guided only by knowledge of a species biology, and if available, empirical baseline data that specify spatial and temporal patterns of movement (e.g., from radio-telemetry, track transect surveys, etc.). The size of the area, geometry, physiography, and the degree of behavioral fidelity exhibited by different species should be considered. Topography is of paramount importance in a mountainous environment because of its influence on climate, habitat, and travel impediments (see p. L-31, Tables 3-6 in Sitka black-tailed habitat models for an excellent example of the type analyses that need to be conducted). In the preliminary analysis any proposed locations of building, roads, or plans for logging should be purposively disregarded. Because land use

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policies influence the availability and quality of movement corridors by affecting habitat availability and effectiveness, planners should identify current permitted uses of the landscape and the associated effects of wildlife management practices.

Initially, we can assume that in undisturbed conditions wildlife movements are the product of an individual or group's search for life requisites. Movements are affected by species adaptations, population size, demographic structure, interspecific relations, the abundance and distribution of food, availability of habitat for security, physiography, and climate. In addition, some movements appear to be learned behaviours. For example, seasonal movements of many species have been shown to follow traditional patterns with seasonal fidelity to respective summer and winter ranges.

We can also assume that for some species, in the absence of landscape disturbance, movement routes will become highly traditional over ecologically significant time periods; not just the location of the routes, but temporal patterns of use along those routes. There is good evidence that among long-lived species knowledge of travel routes is passed down by tradition from generation to generation. (Minta, pers. commun.). Thus, the exact position of the corridor is crucial for some species.

Summer and winter travel for many species appears to be governed by elevation, with river valleys and low elevation passes the favoured routes. In mountainous environments there is increased potential to move in summer because snow depths do not preclude use of high elevation habitats and passes. There is an increased use of low elevation valleys during winter. Frozen rivers and lakes, ridges, and shorelines are used disproportionately because of ease of travel. Ski trails, snowmobile trails, graded roads, and packed roads can artificially enhance the range and efficiency of winter movements (Paquet *et al.*, in prep).

Within this context, the major valleys in the Tongass may function as core areas for a large number of mammals and serve the important role of connecting substantial areas of habitat. Valleys may also allow wildlife to make seasonal movements to exploit patches of food. For ungulates and large carnivores, the valleys and drainages probably facilitate dispersal and serve as corridors for movement between upper elevation summer range and lower elevation winter range.

General Considerations For Design of Movement Corridors

- Rates of successful dispersal from one area to another decline when distances between blocks of suitable habitat increase;

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- Different corridors are appropriate for different landscapes;
- Different corridors have different functions;
- Specific locations along corridors are likely to serve different purposes;
- Different species have different corridor requirements;
- Requirements for different species vary with the degree of tolerance for humans and their activities;
- Individuals of the same species are behaviorally variable; and,
- Social species are prone to develop traditions that vary widely.

Stresses that May Impair the Function of Corridors

Increasing exploitation of natural areas introduces permanent habitat alteration, permanent habitat removal, landscape fragmentation, and establishment of structures. The most significant and pernicious threats to wildlife are related to loss, alienation, and alteration of habitat resulting from establishment of permanent facilities and development of supportive infrastructure. In many cases, the permanence of facilities forecloses future opportunities for restoration. Structures and related activities result in fragmentation of the landscape, occlusion of essential regional dispersal corridors, and impediments to inter- and intra-territorial movements of animals. Barriers such as roads are direct and increasingly important causes of wildlife mortality.

Potential disturbances to corridors include extractive resource exploitation (e.g., mining, forestry), development of utility corridors, roads, air and water pollution, recreational development, and activities such as hunting. Associated with these physical changes are dispersed and transient human activities that alter the behaviour of and habitat use by wildlife species (alienation). The combination of direct habitat loss and sensory disturbances has the potential to obstruct seasonal movement patterns or increase vulnerability as animals attempt to learn new travel routes. For example, human activity may disrupt the timing and rate of movements through a preferred corridor. With increased stress (human harassment, etc.) wildlife may select (or be displaced to) suboptimal travel routes in more difficult terrain, but not without consequence. Depleted energy budgets and reduced fitness are possible outcomes of using secondary routes.

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In designating corridors it is important to remember that we do not know how close animals using corridors already are to a "threshold level" of disturbance, in which direct and cumulative effects will result in disrupted movements. The specific conditions in which wildlife are either "disturbed" or "undeterred" are highly variable. The extent and intensity of disturbance appears to vary with the environmental and social context and the individual animal. For example, there are cases where deer or grizzly bears could not be harassed away from an area, whereas at other times they are easily disturbed.

The behavioral response to disturbance is extremely variable, both inter- and intra-specifically. Much of the variability is believed to be due to complex interactions of direct, indirect, and additive effects. However, there is general consensus among researchers that the response of species to a particular disturbance depends largely on disturbance history. This is a critical concept in understanding the behavior of long-lived animals and social animals that learn through social transmission. It is worth noting that several of the species in the Tongass are both long-lived and social.

Adding disruption to an existing disturbance regime will likely have the least effect if the record of past disturbances is of similar type, frequency, and duration, such that habituation has been allowed to occur. The danger is that the addition of new disturbance may exceed an unknown threshold, possibly due to indirect or cumulative effects, producing an unanticipated outcome. That is, the new disturbance, in conjunction with established background disturbance, may surpass the level of habituation or innate behavioral plasticity that allows animals to cope with disruption. An important variable is how similar the types of disturbance are - as perceived by the animal being disturbed (Minta, pers. commun.). That is, instead of an incremental or quantitative change that merely increases disturbance intensity or rate, disturbance to the animal's environment may be qualitatively different from any in its history, again resulting in unanticipated response (S. Minta, pers. commun.).

General Observations

There is an overall lack of empirical information specific to the Tongass.

For the most part, species interactions are ignored.

On the subject of terrestrial species that require special conservation plans: In general, carnivore populations have a higher probability of extirpation than most other species because they are more susceptible to disruption. Carnivores are generally less resilient than ungulates because of limited reproductive capacity (unlike ungulates they did not evolve to sustain high rates of mortality, and therefore there are fewer animals at higher trophic levels). The larger carnivores have been identified as being most at risk, primarily because of

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low numbers and reduced distribution owing to extirpation and displacement (Hummel, 1990).

In determining the extent of disruption that may occur as the result of human activities: Hunted populations of wildlife usually avoid human disturbance. Alienation of habitat often occurs as a result of displacement to avoid sensory disturbances. Reactions to noise and human activity vary with local conditions and circumstances, but the response generally is movement away from disturbance.

Individual wildlife species were treated very differently as reflected in the uneven quality of the models. The brown bear model was comprehensive and current, whereas the wolf model failed to incorporate recent information. I would have to question the efficacy of the modelling procedure without an effort at validation.

Are minimum viable populations to be maintained into perpetuity? Why does the conservation plan stress minimum viable instead of just viable? Why the short time frame for modelling of minimum viability?

I would like to see an effort to determine available habitat for different species after excluding unusable areas (rock, ice, some slope and aspects). I would also like to see criteria for establishment of corridors that include width, cover, configuration and geometry.

There is general acceptance that road density is one key predictive variable which can be applied when estimating the effects of disturbance and habitat fragmentation (Noss, 1990; Lyon, 1984; Mattson *et al.*, 1987). Although there is variability in the literature with regard to the amount of displacement and other impacts, there is irrefutable evidence that roads and disturbances associated with roads reduce habitat effectiveness resulting in reduced fitness and increased mortality. Briefly, roads fragment wildlife habitat, reducing the habitat's capability to provide security for wildlife. This results in wildlife avoiding or underusing the fragmented habitats or being exposed to elevated risk of mortality, thus reducing habitat effectiveness. Consequently, more emphasis should be placed on the potential negative effects of roads.

Wolves - Conservation Strategy

All sections pertaining to wolves are limited and somewhat outdated. However, the viability risk assessment, species account, and conservation strategy are probably adequate, considering the lack of empirical information available for the Tongass. The species account and conservation strategy could be improved by including more recent and possibly relevant literature. A more

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complete discussion of some of the biophysical factors that influence wolves would also be appropriate (see below).

The outlined objective of sustaining viable populations of wolves in the Tongass is unrealistic. As large as the Tongass may be, the area is probably too small to maintain the numbers of wolves required for long-term sustainability. A more reasonable (and realistic) conservation objective would be to maintain the ecological processes and components that are essential for securing the future of the wolf population now occupying the Tongass. This means that population viability will have to be addressed in a regional context, with an effort to maintain linkages with "subpopulations" of wolves in other areas. Because the Tongass does not exist in a vacuum and is not a self-sustaining system, the U.S. Forest Service will need to develop plans that address transboundary and interjurisdictional movements of wolves. To be successful, such an effort will require close cooperation with the state of Alaska, as well as Canadian federal and provincial agencies.

There are several reasons why I believe the Tongass is of inadequate size to maintain a viable populations of wolves. As noted, in the proposed conservation strategy, densities of wolves vary according to available prey biomass and social factors that inhibit reproduction. Wolves are true apex predators that are dependent on ungulate prey for their survival. Consequently, their densities are often much lower than other predators that can successfully function at several trophic levels (e.g., bears). Moreover, the hierarchal social system of wolves tends to reduce the effective breeding population far below the actual number of wolves that may be present in an area.

Intertwined with these factors are landscape elements that restrict usable habitat and thus population density. For example, topography influences accessibility and quality of habitat for wolves and their prey. Two examples serve to illustrate the effects of topography on wolf numbers. My study area in the Canadian Rockies is a bit larger than the Tongass and contains 11 packs and < 100 wolves. Less than 22% of the area is usable by wolves and their prey. As would be expected, much of the study area is covered with rock and ice. In contrast, the highly productive and topographically homogenous area of Riding Mountain Nation Park, Manitoba supports ~65 wolves (845 wolves if extrapolated to 16 million acres). Nearly all of the area not covered by water is usable, and frozen waterways become available in winter. Accordingly, I would guess the topography of the Tongass probably restricts effective habitat for wolves to less than eight million acres, most of which is in lower elevation valleys targeted for logging.

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Habitat Capability Model

The habitat capability model is next to worthless in its present form. I am particularly concerned that forest managers will make decisions based on conclusions derived from this model. Although the authors clearly acknowledge that the reliability of habitat capability models is questionable, the point has not been emphasized strongly enough. This cautionary note is important and must be conveyed to decision makers if the wolf habitat model is to be retained in the final conservation strategy.

However, given the lack of data on wolves in the Tongass, I am convinced that habitat capability modelling is not worth the investment of time or money. Moreover, in the absence of good information the risk of misapplication of the model is increased. I question whether we learned anything from this model and whether it assisted in the preparation of a better conservation strategy? I suppose that at the very least it revealed the paucity of information available for the area. Notwithstanding the previous comments here are several suggestions that may help improve the current model.

1. Beaver are not available throughout the year so they should be only considered an alternative prey that are available seasonally. Moreover, my experience has been that beaver may be seasonally important in terms of numbers killed but not biomass consumed.

2. The model does not incorporate community level interactions. As an apex predator the wolf has profound effects on the environment. At a minimum, the model should consider secondary consumers (scavengers) and competitors such as brown bears.

3. The model should address the ability of alternate prey to sustain wolf populations at low levels.

4. The role of salmon should be considered, possibly in the same way beaver are incorporated into the model.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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I reviewed three documents: 1) *A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska. Report of an Interagency Committee* ("*Strategy*"), 2) the chapter on wolves in *Habitat Capability Models for Wildlife in Southeast Alaska*, and 3) *Appendix M. Fish and Wildlife: A Viability Risk Assessment.*

1. Background

I grew up in a rural setting in Minnesota with a fishing pole in my hands. My early summers were spent at my grandparents' cabin on a lake in northern Minnesota. My dad had an acre of land he wasn't using when we were in high school, so my brothers and I planted it with tomatoes and paid for much of our undergraduate education with truck farming.

My academic background includes a B.S. in Wildlife Management at the University of Minnesota in 1974, an M.S. in Wildlife Biology at Kansas State University in 1977, and a Ph.D. in Forestry (Wildlife Ecology) from the Yale School of Forestry and Environmental Studies in 1982. I worked for almost a year on the Isle Royale moose project between my B.S. and my M.S., and taught at the University of California, Berkeley as a sabbatical replacement before taking a tenure track position at the University of Montana. My academic background and research and teaching experiences have become less game-oriented since my B.S. and more oriented toward a broader definition of wildlife conservation. I currently supervise and/or participate in research on endangered species (wolves in Montana and adjacent British Columbia, several species including wild yak and argali in Qinghai Province, People's Republic of China), biodiversity (effects of stand management on diversity of mammals in western Montana), as well as game species (impacts of wolves and other predators on white-tailed deer, elk, and moose).

The philosophical text that has guided me most in my work is Aldo Leopold's "A Sand County Almanac". I believe conservation is fostered when

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people view themselves as being a part of, as opposed to apart from, nature. I would place both dominionistic people (resources are wasted if not used) and humanistic/moralistic people into the same group who view humans as being fundamentally different and apart from the rest of the biotic community. People are the cause of most conservation problems, and involvement by local people is necessary if these problems are to be resolved. This type of bottoms up approach to conservation (as opposed to a top down approach) is espoused by much of the international wildlife community, and is also very important in North American conservation.

Leopold's famous quote from "A Sand County Almanac" where he defined proper land use and a land ethic is key: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." This is interpreted to mean insuring the continuance of species, using resources in a sustainable fashion, and maintaining the evolutionary and ecological processes that comprise beauty.

My professional memberships include The Wildlife Society, the Ecological Society of America, and the Society for Conservation Biology. I have been fairly active in The Wildlife Society, especially in international affairs.

2. Comprehensive Review

I applaud the efforts of the compilers of this document for their efforts to address biological diversity on the Tongass. That is not an easy task.

I do, however, have suggestions, both general and specific. Early in the document, it is stressed that this is a very diverse and "naturally" fragmented environment. There are many islands and inlets, and impressive elevational gradients, resulting in what must be dramatic differences in vegetative growth. It is difficult to assess fragmentation caused by human actions without a good idea of the matrix currently on the land. Some of these "old-growth" stands are much more productive than others (some contain greater than 50,000 bf/ac). A simple statement that 6.7% of the productive old-growth (productive defined as > 8,000 bf/ac) has been cut since 1954 doesn't tell us much. A large proportion of the forest is designated wilderness. What proportion of the stands with greater than 50,000 bf/ac have been cut? These highly productive areas are likely to have been most heavily cut-over, and to be highly productive for wildlife, as well. What proportion of the low elevation areas have been cut? How does the spatial pattern of cutting mimic or not mimic the naturally fragmented environment?

Conservation of biological diversity should involve more than just species. Higher levels of biological organization (habitat types, communities, and ecosystems) should receive more attention.

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I understand the need for discrete habitat conservation areas in a case like the spotted owl where the landscape has already been greatly impacted. The *Strategy* document states that only 6.7% of the productive old-growth has been harvested, however (i.e., 93.3% still remains). Why implement a plan where only islands of suitable habitat within an archipelago remain? Relatively small HCAs should be a last resort in conservation planning. It seems to me that the process should work to avoid fragmentation in the first place. Management should be directed toward avoiding the situation depicted in the habitat conservation areas map. Something close to the inverse of this map, where white areas are the habitat areas and the colored areas are more highly impacted areas, would ensure connectedness, and allow species to freely move within (and occasionally between) the islands upon which they are found.

Barring the approach described in the preceding paragraph, much more emphasis should be placed on the land between habitat areas. Dispersing animals will not have a map of where the nearest conservation area happens to be, but it would seem logical that their survival will be enhanced, and their probability of finding suitable habitat increased, if the area between habitat areas would support these species for as long a period of time as possible. Discussion of these areas is minimal toward the end of the strategy. There are few empirical studies documenting the value of narrow corridors.

Regarding the selection of species for review, I would suggest that more information is needed on those species whose occurrence on the Tongass represents the geographic edge of their distribution. Preventing the reduction of the overall geographic range of a species can avoid future problems elsewhere. By insuring the continued existence of these species at the edge of their range, their core populations may be more likely to be assured, as well. These species are most likely to be affected by habitat changes and may be good indicators of what is going on. The Tongass is large, but what happens here has impacts on surrounding ownerships.

I would need much more time to evaluate the model used to select species of concern. There would seem to be important interaction terms necessary. For example, a species whose distribution was limited to SE Alaska and whose population was low should, by those two criteria alone, deserve special recognition. Conversely, a species whose distribution was limited by non-anthropogenic factors to SE Alaska and whose population was high may not deserve special recognition. The 60% level of concern seems arbitrary to me, especially since two other species, the boreal owl and the Vaux's swift, are at 60 and 59%, respectively. Why aren't they included? Also, are plant species adequately covered?

Even the large habitat conservation areas are quite small. At 40,000 acres, they are probably too small to contain one wolf pack. Why have HCAs within wilderness areas since no management activities will occur there anyway? These

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larger blocks of habitat are very important to conserving many species; their role seems to be minimized by placing HCAs within them.

Ecological provinces are a good place to begin with an assessment of the effectiveness of the HCAs, but a stratification by a finer habitat criteria (see above) would also be appropriate.

Under objectives for large HCAs, what does "limit timber harvest" mean? At 40,000 acres, 20,000 of which must be at old-growth with at least 8,000 bf/acre, that leaves 20,000 acres. What are the objectives for the remaining 20,000 acres? How much timber harvest will be allowed, and what prescription will be used? The same questions apply to the medium and small HCAs. On page 30, the issue is further confused (to me) with the statement that "timber harvest (except of limited second-growth and salvage) should not be allowed within the HCAs. Silvicultural treatments that have been demonstrated to enhance important habitat attributes may be appropriate within HCAs." Where within HCAs? I would try to limit salvage cutting even further. These downed logs provide important components of the habitat in old-growth, especially for small mammals, and should be retained whenever possible. Hiding cover along roads within HCAs is probably as important as clearing width, especially for wolves and harvested species.

Under Additional Standards for Species of Concern, for great blue herons, shouldn't disturbance be prohibited while nest activity is occurring? Shouldn't timber harvest be restricted throughout the year and not just during the nesting season? I will comment more extensively on wolves below.

The Viability/Distribution Risk Assessment briefly considers the quality of habitat between HCAs. Given how important that is, I think much more emphasis should be placed there. That is also a better place to start assessing where HCAs should be placed (see above). Risk would be greatly reduced if the white areas on each of the islands were the HCAs (see above).

It sounds to me (p. 41) that the ASQ needs to be reduced.

3. Species Review - Wolf

Wolves are covered on pages G1 - G13 of the *Habitat Capability Models*, and from pages 156 - 170 of the *Strategy*, and I will discuss them together.

The recent review of wolf taxonomy by Nowak (1993) does not recognize *Canis lupus ligoni* as a valid subspecies. The review suggests that there are only five subspecies of wolves in North America. This does not, however, lessen the need for conservation of this species. In the contiguous 48 states, breeding populations of wolves are found in Michigan in addition to the states mentioned.

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The weights of fawns and calves presented were apparently taken during their first winter. Many fawns and calves are killed and eaten long before winter when they are much lighter. More young must be killed during summer to meet wolf consumption rates. In our study area, where the primary prey of wolves is white-tailed deer, survival of adult females is almost 100% during summer (Rachael, 1992). Low fawn:adult ratios and limited analyses of wolf scat suggests that fawns are a significant summer food. This occurs at a time when fawn weights are 5 - 10 kg. The overall number of deer killed must be higher in summer (with their lighter weights then) than during winter. The same could be said for moose and mountain goats.

During winter, snow depth can significantly affect consumption rates: in deep snow winters, consumption rates are significantly lower (Boyd *et al.*, 1994:in press). This can greatly increase kill rates.

Distribution of black-tailed deer will not be uniform across the landscape, especially during winter. As in other discussions above, this spatial pattern is very important. Areas without prey during winter will not have wolves.

Twenty percent of the overall deer population available per year for consumption by wolves is pretty high, especially in an area where there are other predators on deer (humans, and occasionally, especially on fawns, brown bear, black bear, and lynx). Ten to fifteen percent would be a safer figure, but don't expect a stable predator-prey system (see Botkin, 1990). This, in addition to lower consumption rates during deep snow winters, would increase the needed deer density to at least double the 5 deer/sq. mile.

Road densities should be kept below 1 mi of open roads/square mile whether they are accessible (whatever that means) to communities with populations greater than 1,000 people or not. In our study area in northwestern Montana and southeastern British Columbia, we have had wolves shot or poisoned on closed roads or old seismic lines. I am not aware of studies on wolves that have made recommendations on closed roads, but I suspect that there should be a limit on closed road density, too, because these are travel corridors for humans. Also, the cover available along roads probably also affects wolf survival. A road passing through a recent clear-cut provides no security for a wolf, whereas a wolf could reach security in one jump off a different road passing through dense hiding cover.

The recommendation of allowing higher road densities near wilderness or roadless areas should be abandoned, at least for the smallest roadless areas. At a minimum size of 40,000 acres, one wolf pack may not have its entire home range inside of this roadless area. A <u>reduced</u> road density adjacent to roadless areas would provide a buffer strip for wolves and other wildlife found there.

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4. Comprehensive Recommendations for the Future

Many of my recommendations were included in the comments above. The idea that I would provide is certainly not new, but if the study area is now relatively intact, keep it that way as much as possible. Consider using development areas of roughly the sizes, shapes, and juxtaposition of those that have been designated as HCAs, which would leave most of the archipelago intact. Use more detailed information on plant communities and productivity, in addition to the Ecological Provinces, to ensure representation of all of these types in conservation areas.

Consider keeping track of more species. Two other species, the boreal owl and Vaux's swift, are too close in sensitivity (given the model used) to not include.

All of the sensitive species should be monitored within subunits of the Tongass so that impacts of the Forest Plan can be assessed. Obviously, different monitoring plans must be used for each species. For wolves, track transects can be used to estimate presence or absence of wolves. Radio collaring 2-3 members of each pack and occasionally flying over them and counting pack members could be used to monitor populations.

Given the variable sizes and distances of habitat patches and islands to each other, an adaptive management approach (Walters, 1986) would seem to be appropriate. Replicates of careful management prescriptions, with monitoring of wildlife populations before, during, and after implementation, could, if designed properly, result in meaningful improvements in future management. It could also provide insights into the effects of habitat fragmentation on wildlife populations that may have ramifications elsewhere.

5. Species Specific Recommendations for the Future

Recommendations for wolves were given above.

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Tongass National Forest
Land Management Plan

Scientific Review

by

Roger A. Powell
Professor, Department of Zoology
North Carolina State University

1. Background

My background and my research has been at the interface of population biology, ecology, behavior and evolution and my research has focused on how limiting resources affect individuals, populations and species. Moving between field research, simple modeling, and lab research has, I believe, given me insight I could not get from any single approach. I strongly believe that research on wildlife must be grounded in theory. And I believe that theory must be tested on wildlife and not tested only on small animals from whom it is easy to collect much data. If our theory is robust, it will apply to wildlife and it will give us strong insights into unknown aspects of the biology of wildlife. This is, perhaps, not a surprising approach for someone who has always been intensely interested in understanding the biology of wildlife and who attended the University of Chicago while Dan Janzen, Monte Lloyd, Dick Levins, Dick Lewontin, Monte Slatkin, Steve Arnold and Mike Wade were there.

Although management decisions are best made from a solid understanding of the biology of managed species gained through good research, I also understand that for political and sociological reasons, management decisions must sometimes be made without such background. Management decisions must be made within the context of society. All scientists, and certainly biologists, have the obligation to educate society so that value judgements can be made in an informed manner.

With respect to this review, I believe that my background is appropriate. Over the past 25 years, I have done research on fishers, weasels and other members of the weasel family, and on black bears. I have helped states write management plans and I helped revise the Recovery Plan for black-footed ferrets. I believe it is our obligation in this review to provide managers on the Tongass National Forest with the best biological background for making decisions.

The documents are sometimes wordy and contain poor grammar in places. I have marked some of these places on the copies I received. Split infinitives were

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not uncommon and sometimes confusing. References to pages and to other sections were often blank. Tables, figures and appendices were sometimes missing. Some cited literature was not in the Literature Cited sections.

Why have minimum viable populations been chosen as a goal? The goal should be to maintain healthy populations far above minimum. If planning is for minimum populations, that is what will be obtained in due time. Therefore, these documents should propose a broad plan that determines what sizes of populations are "optimal" and has those population sizes as the goal.

A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska

General Comments

I found the overall tone of this document disturbing. The document appears to have been written under the assumption that logging will continue at a rate harmful to wildlife and, within that context, the best must be done to minimize the chances that wildlife populations fall below minimum viable population levels. Under the National Forest Management Act, however, wildlife are considered an important component of national forests. Therefore, I would have preferred to have read a document that sought to understand what is needed for wildlife under different conditions and to determine at what levels of logging wildlife resources would be optimized. I would prefer to see a document that looks at "optimum" population sizes for wildlife and then juggles both logging and wildlife populations to find a level of logging that meets requirements both for wildlife and for logging. Determining "optimum" wildlife populations requires an understanding of what is "optimum" for different people. Some wildlife are trapped for fur, some are hunted, some draw tourists to Tongass National Forest, etc. I see no reason why these values of wildlife should automatically be valued lower than logging. Nor should logging automatically be sacrificed for these wildlife values. I wanted to read a document that struggled with this concept and led to a solution, rather than to read a document that emphasized salvaging wildlife given that logging will continue. Wildlife are integral to a forest; a forest is not a forest without them.

The 17 "Evaluation Criteria" seem fine for starters. The weighting factors applied to them are not always justified, however, and sometimes appear to defy logic. For example, it does not make sense to choose weightings that lead to choosing a common species that is at the edge of its range in southeast Alaska while an endangered, endemic species is not chosen. Criteria 10, 11, 14 and 17 should have higher weightings. Criterion 12 should be weighted higher, too.

For example, Great Blue Heron and Boreal Owl do not appear appropriate for this plan. These species are at the edges of their ranges in southeast Alaska

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and could become locally extinct for many reasons not related to habitat manipulation by the Forest Service. Endemic species should be included here, not abundant species at the edges of their species ranges.

In addition, the Evaluation Criteria are not independent. Therefore, some thought should perhaps be given to choosing criteria that are as independent as possible or to applying factor analyses, or some other multivariate statistical analyses, to the criteria to find underlying, independent factors.

On page 91 there is the statement: "It is critical in this approach that the habitat patches be numerous enough and close enough together to ensure that the species of interest will be able to disperse throughout the network." I am not convinced that this document guarantees such dispersal. I am concerned about the distances between HCAs. Spacing large HCAs at 20 mi and medium HCAs at 8 mi seems excessive to me. Data on movements of transient martens, for example, document that martens can travel these distances but not necessarily under the conditions to be found on the Tongass National Forest a decade or two from now. A marten travelling from a large or a medium HCA could travel through country over 75% of which is not HCA and therefore could be extremely poor habitat. A marten travelling in a straight line radius from an HCA could have a 75% chance of not hitting a large or medium HCA after travelling 20 miles. Thus, the spacing of these HCAs is excessive for any normal dispersal or gene flow between the watersheds designated as HCAs.

The distances and areas chosen for protection are not well documented. For example, protecting 1/8 mi (200 m) around a heron rookery and 1/4 mi (400 m) around a goshawk nest are proposed but no documentation for these distances are given. Elsewhere in the materials I reviewed I found some references to distances such as these but I could not cross-check all of them to be certain that all such choices matched reported data. Better documentation is needed. At least one example exists where the proposed distance for protection is distinctly different from what is suggested by data (brown bears: 75% of activity within 200 m of streams but only 100 m buffers proposed). This makes me wonder if documentation was avoided at places in this document in order not to have to justify choosing protection distances that contradict data.

Many references are to USDA Forest Service documents that are not readily available and which, I presume, did not receive peer review. These are not strong references on which to base a management plan.

Specific Comments

pg 23, 4): This is an example of allowing logging to affect approaches to wildlife (adjusting HCAs to minimize impact on logging). Although I agree with

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this step, I believe it should be at the very end of the entire process and should come after serious consideration is given to reducing logging.

pg 29, Objectives: I question whether a female marten would remain in a small HCA. The designated area is just the estimated home range size for a female marten when vole and hare populations are low.

pg 29, Travel Corridors: This is a good paragraph. It states clearly that little is known about whether wildlife use travel corridors. It states clearly that areas designated as "travel corridors" may not function as corridors for wildlife at all and that other options are necessary for wildlife dispersal and movements. The conclusion, that maintaining links between areas of good habitat is easier than reconstructing such links, is also right on target.

pg 30, Objective and succeeding para: Given the preceding paragraph, why was the matrix approach dropped? The preceding paragraph made clear so poignantly that multiple approaches are needed and the corridors may very well not work worth beans. Why drop the alternative approach?

pg 30, Standards, 1): This sounds like a way around saving habitat for wildlife - designate HCAs, log all around them, designate new HCAs in the logged areas, log the original HCAs. The intent of this standard may not be to allow wildlife habitat to be logged, but this standard may have that function.

pg 31, 3): Why "salvage" downed or dead trees at all? Wildlife need these logs and trees. Martens need such logs and trees, especially. "Salvage" is a term that only has meaning here in the context of logging. Dead and downed trees are important resources for many wildlife and should be left for them, not stolen from them. This section could be revised to say that dead and downed trees will only be stolen from wildlife under the specified conditions. Such a revision would be no more biased than the present wording.

pg 32, last line: A time limit should be designated for obtaining adequate data on goshawk home ranges and core areas, in case the protected areas are inadequate.

pg 33, Gray Wolf, 1): I do not understand the limits on roads. I think this section says that the mean density of roads on any three contiguous Wildlife Analysis Areas is not to exceed 1 mi/mi^2. This means that a large proportion of these areas could have road densities exceeding this limit as long as other areas have densities low enough to bring the mean under 1. This will not work. Wolf populations decline where road densities exceed 1 $mi/mi^{1/2}$. Under this criterion, large sections of Wildlife Analysis Areas could become not wolf habitat.

Unless there is no way that anyone could get an ATV or ORV onto a road or that anyone could hike the road, all roads should be included in calculating

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densities. All roads, even roads open only for hiking, increase human use and therefore have negative effects on predators. My experience is that management agencies are far more willing to call a road closed than are the people who want to use it. Roads designated as "closed" in my black bear study area get regular vehicle use by people who have found ways to get around the blocks.

Road density next to wilderness areas should also be 1 mi/mi^2.

And what is a "Wildlife Analysis Area"?

pg 34, 4): Road density limits for brown bears should be the same as for wolves: 1 mi/mi^2.

pg 39, para 2, line 2: Why have minimum viable populations as a goal? The goal should be to maintain populations far above minimum. If planning is for minimum populations, that is what will be obtained in due time. Therefore, what is really needed is a broad plan that determines what populations are "optimal" and has those as the goal.

pg 114, para 1, last sentence: If the recommendations are important enough to be mentioned here, then they should be summarized. If they are not important enough to be summarized, then they should not be mentioned here.

pg 156 - Wolf: The tone of this section is negative. I read this section to say that wolves are going to decrease in densities because of logging and may disappear. But it is my understanding that this document is supposed to outline ways that wildlife populations will not be decimated. Therefore, this section should instead outline the necessary steps to ensure that a healthy wolf population remains in as much of southeast Alaska as possible. The optimum wolf population size should be determined, considering wolves as a fur resource, as a tourist resource, and as an animal important to residents of the US who live elsewhere.

pg 158, last para: Why emphasize the ability of wolves to hold prey at low levels? This has little or nothing to do with this document. This paragraph appears to me to be a response to the public concern about the killing of wolves elsewhere in Alaska. This document is not the proper place to attempt to justify that action.

pg 161, para 3, sentence beginning "For example,": This sentence contradicts itself. If fewer than 11 wolves have been harvested annually since 1984-85, then 22 could not have been harvested in 1989- 90. Alternatively, if 22 were harvested in 1989-90, then more, not fewer, than 11 wolves have been harvested in at least one year since 1984-85.

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pg 165, 2): How does this density of deer compare to the density of deer before logging began? Is it a decrease or an increase in density?

pg 171 - Brown Bear: I gain a similar feeling from reading this section as I did from reading the wolf section. I find it negative instead of positive.

pg 171, second to last sentence: Why do the authors consider the present units too large? Do they mean there are too few of them, each too large? Or are the authors arguing that logging needs will require the units to be smaller? I am confused here and am not convinced that the authors are trying to outline a plan that has at heart the best for brown bears.

pg 172, 3): I assume this means 100 m buffer to each side of each stream. But why only 100 m? On pg 187, bears are documented to stay within 200 m of streams. Here is an example where lack of good documentation causes trouble.

pg 176, para 2: It should be highlighted that this model has not been tested, and therefore its ability to predict habitat for brown bears is unknown.

pg 177: The large HCAs are clearly too small for brown bears. If male home ranges average 100 km^2, even with extensive overlap there will be few males in an HCA of 165 km^2 (40,000 ac). Home ranges of adult males tend to overlap less than those of adult females, and may overlap little. Thus, each large HCA will not maintain a minimum population of brown bears.

pg 178, lines 3-5: How long was Schoen's and Beier's study? If it was short, then 28% could be a high number. If their study was long (decades long), then 28% would be a low number. Perspective is needed here.

pg 178, para 2: Table 1 is missing.

pg 179, last word: Should this be Appendix C1?

pg 180, para 2, sentence 2: Faster than what? I thought site-specific data were being used in the first place. Why were they not?

pg 182, para 2, end of para: Here, again, is planning for a minimum population. Planning should be for higher populations, not to salvage populations after logging has occurred.

pg 183, lines 3-5: Were the roads built and timber harvested in 1992?

same para, last line: Why were no plans made for mitigation?

pg 186, line 1: One mile, 1.6 km, is not far for a bear.

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pg 186, para 3: Does industrial development include logging?

pg 186, last para, sentence 3: No seasonal exceptions should be allowed for road closure. Road closure must be absolute and complete.

pg 187, sentence 1: What are the employee policies regarding firearms? They must be specified here if they are to be mentioned at all. If the policies are not worth specifying here, then they should not be mentioned.

pg 187, para 2: Here is the documentation that brown bears are within 200 m of streams 75% of the time. So why on earth should buffers be only 100 m on each side of streams? If the buffers are meant to be only 100 m wide, 50 m on each side of streams, then this is 1/4 of the minimum appropriate width. I could argue that an appropriate buffer should actually contain the 90% or 95% limits.

pg 189, 1): The dump bears probably are the "wild" bears.

pg 196, last para: Given that male home ranges average 100 km^2, it seems that in 1000 km^2 there would probably be at most 20-30 adult male bears. This number approaches a minimum population size for conservation.

pg 212, para 3: Data should be presented here showing that martens in southeast Alaska do not use high elevations. In the Rockies and in the Pacific Northwest, martens use high elevations, not low elevations. Why the difference? What are the ecological reasons?

pg 217, 1.: No such thing as a "reproductive unit" of martens exists. This is a complete figment of the imaginations of management personnel. Martens have never heard of it! Martens maintain home ranges independent of all other martens and do not maintain social bonds beyond the mother-offspring bond. All mention of "reproductive unit"s must be deleted. Any thinking or planning along these lines must be rethought and replanned. To do otherwise is asking for future problems.

pg 218, 3.: 570 ha is smaller than the mean home range size for male martens and almost half the size of the home range sizes expected when prey populations are low. Thus, 570 ha is meaningless as a management unit. High quality habitat becomes low quality habitat when prey populations crash.

pg 218, Yukon Territory: Reserves 92 km^2 in size are reasonable. Reserves of similar size spaced at 9.6 km intervals would be fine in southeast Alaska.

pg 220, last para: Why put an upper limit on HCA size? This makes no sense to me. The spacing of 40 km between HCAs is too long a distance; setting this distance at maximum dispersal distance makes no sense. Same goes at the top of pg 221 with medium HCAs.

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pg 221, para 2, end: The distance a marten will actually have to travel to get from one HCA to another will exceed those given here by much. Martens will not know when leaving an HCA what the direction is to the nearest HCA. Thus, martens could conceivably travel very long distances, going between HCAs. I suspect that this will happen most of the time.

pg 221, para 3: The recommended small HCA size of 6.5 km^2 is smaller than a male marten's home range when prey populations are high. Therefore, small HCAs must be much larger.

Appendix M

General Comments

I found this document also to be generally negative. It seemed to me to outline a plan that guarantees that wildlife populations on the Tongass National Forest will be lost in the future. The document, instead of testing what management plans will guarantee that wildlife populations will exist in perpetuity, documents how wildlife populations will be lost. The document takes for granted that the level of logging on the Tongass can not be changed, despite the negative effects the logging will have on the wildlife. To me, this whole approach is backwards. National Forests have multiple uses. Forests without wildlife are no longer forests, but agricultural fields that grow trees. There is no reason why a management plan can not be developed that allows logging and also allows the perpetuation of wildlife species native to the Tongass National Forest.

Specific Comments

pg M-9, para 1, last sent: It may be that behavior of individual animals must be documented to understand habitat suitability.

pg M-9, para 3: This paragraph slips into the assumption that what the habitat capability models and habitat suitability models predict is correct. The first sentence must specify that it is "predicted quality" that can be compared. Later in the paragraph, the authors must not fool themselves that they ever can validate a model. Models can be tested and found better than the null hypothesis of not being able to predict anything. But models can never be validated as being perfect predictors of habitat quality or capability for wildlife.

pg M-11, sentence 1: What is "productive old-growth"? "Productive" means different things to different people.

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pg M-13, 2.: "Travel corridors" are unproven. Until shown to work, it should be made clear that corridors are hopes, not knowns.

pg M-19, para 1, end: How were HCAs changed? I would like more detail here. What criteria were used in deciding that the HCAs should be changed?

pg M-43, para 1. The short-term risks are only high if the standards and guidelines of the forest plan are not followed. To me, this means that the risks should be assumed to be high because I assume that the standards and guidelines will not be followed closely. This means, in turn, that something must be done to guarantee that short-term risks are not great, something other than is presently being done.

Habitat Capability Models for Wildlife in Southeast Alaska

General Comments

The author's comment at the top of pg i-4, that these models are to be used for planning, is a good one and one that provides an important perspective. Decisions will be made, with or without adequate information. Therefore, these models need to be as good as they can be because they will be used.

I was surprised that no reviews or comments on the models were received from researchers across the continent who are actively working with these species. For each species, several researchers whose publications are cited should have been contacted. Many of the researchers whose publications are cited have worked on these species in Alaska or are familiar with the conditions on Tongass National Forest. Having contacted those researchers would probably have strengthened the models considerably.

It is not clear how roads, dumps, and other sources of contact with humans are incorporated into the computer programs at the ends of the chapters on the wildlife species. These are important components of the habitat capability models for both bears and for martens. It appears, in fact, as though the negative effects of these human components have not been included in the computer models at all. I find this a bit scary. If this exceedingly important aspect of the habitat capability models is not included in the computer models, what else has been omitted? Can the computer models be trusted at all to mimic the written explanations of the habitat capability models? If the computer models are missing important components, what good are they?

Nor is it clear how juxtaposition and interspersion of habitats are included either in the verbal habitat capability models or in the computer models. These appear to be mentioned in the text and then dropped, despite their importance. Did the authors assume that juxtaposition and interspersion would not be

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problematic and therefore could be ignored in the computer models? If this is the case, it must be justified. As habitats change, as is projected because of logging, juxtaposition and interspersion of habitats will change. Therefore, these must be incorporated into the models.

Why were sensitivity analyses not performed for all models? Elasticity analyses should be performed as well. These analyses must include the effects of roads and other human activities.

Arthur Allen has published a habitat suitability index (HSI) model for American martens that is supposed to be applicable across North America. To my knowledge, Allen's HSI model has not been tested but his HSI model for fishers (a congener to American martens) has been tested and found to be reasonably predictive in natural habitats (i.e., excluding plantations).

Because Allen's model exists and should be applicable to American martens on the Tongass National Forest, I see no reason for another model to be developed. Time and other resources would be far better spent testing Allen's model than spent developing a new one. Therefore, before the model proposed here is given much attention, the authors must be able to justify having developed it at all. Because they do not justify developing this model, I can only assume that the authors had no justification for developing it. They cite Allen's model inappropriately; they cite it as an original research report when it is, at best, an incomplete literature review.

On page J-8 the authors incorrectly cite a paper I published. They cite my paper as saying that populations of *Clethrionomys gapperi* remain low for up to 10 years following clear-cutting. My paper, in fact, documents extremely high *Clethrionomys* populations the year following a tornado blowdown. There is no way to know how many other publications have been cited incorrectly. This reduces my confidence in these documents.

The irregularities listed above cause me to be very skeptical of the habitat capability model developed for American martens, and to be skeptical of the models developed for the other species as well. The authors appear not to have done their homework. Their exceedingly simple models require considerable justification before they can be accepted.

I found the use of acres, miles, and other avoirdupois measures difficult to use. Therefore, I found myself constantly converting measures to metric. All of the literature published on these animals in recent decades is in metric. Metric would be the appropriate units for these models.

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Specific Comments

i-4, a): I do not understand the problem with nonmonotonic variables.

i-5, next to last para: I found the discussion of verification disturbing. The word "verification" implies that work is directed towards proving that the models are correct. It is far more profitable to test the models against the null hypothesis that the models do not make meaningful predictions.

ii-5, para 2: The reference to a 0.1 change in nonproductive habitat in the habitat capability model for American martens is out of context. A 0.1 change may constitute a 100% change or more. This is direct confirmation of the need for sensitivity and elasticity analyses of all the models.

same line: "nonproductive forest" does not appear in either the habitat capability model or the computer model for American martens. Thus, this paragraph could be understood to be purposefully misleading.

Gray Wolves

This model assumes that wolves are affected more by characteristics of prey populations than by components of habitat. Except for roads being components of habitat, this assumption is probably true or nearly so. The equations generated from this assumption appear appropriate.

pg G-5, 2nd full para: The citations for the last sentence in this paragraph are all old. Wolves can, at times, deplete their prey populations considerably and are most likely to deplete their prey on islands. Therefore, this possibility should be considered in this plan.

pg G-6, para 2: The assumption that wolves kill prey before hunters do is the kind of assumption that must be made in matrix models of population dynamics. It is well known that the order of events in matrix models has large impact on the predictions of the models. The effect of the order of wolf and hunter kill should be investigated to see whether it affects the predictions of the model. If it does, then some manner of mixing hunter and wolf kill realistically should be done.

pg G-6, before "Equations": Setting a minimum for the wolf population can be dangerous because it prevents predicted populations from going below this minimum. If the assumptions of this minimum are not met, the predicted population size could be an order of magnitude greater than it should be. I suggest that the beaver population be incorporated into the model as have other prey populations. Then, the model would be able to predict very low wolf densities.

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There is a problem in assuming that wolf populations can be maintained at low levels by predation on beavers. Beavers are predominantly summer prey for wolves and are largely inaccessible during winter. Thus, if populations of other prey are low during winter, wolves will not have access to beavers and thus the wolf population can not be maintained by beavers. Beavers must be incorporated into the model as summer prey only.

pg G-6, before "Equations": Why were roads not incorporated into this model as they have been in the models for other predators? Wolf populations fluctuate negatively with road density, as do populations of bears, martens, etc. I suggest that roads be incorporated into this model.

Black Bears

Lynn Rogers (unpublished data) found that black bears in Minnesota, especially females with new cubs, may prey heavily on fawns during the period that fawns hide and do not travel with their mothers. This may be an important source of protein for these bears. Data from my bear research (Seaman, 1993, Ph.D. thesis) provide indirect support for this: adult female bears with new cubs travel more in spring than do other classes of bears. Whether black bears on the Tongass National Forest need fawns as a source of protein is not known. These bears have salmon as a source of protein during the summer, which may reduce the need to prey on fawns.

pg H-17, §c§: Multiplying denning values by 1.5 actually inflates the denning values and makes these values appear larger than they really are. Given that high values indicate good habitat, inflating denning values falsely increases the value of denning habitats. It seems to me that denning values should be deflated or incorporated into the model in a different manner.

pg H-31: From my experience working with black bears elsewhere in North America, the reduction factors are too small for "roads accessible to vehicles", "accessible road within 0.5 mi...," and "road limited to hiking/ORV...". The authors need to justify the reduction factors they used or else, in my opinion, they should lower them.

pg H-35, Appendix H-2: It is not clear how roads, dumps, and other sources of contact with humans are incorporated into the computer program.

How are juxtaposition and interspersion incorporated into the computer model?

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Brown Bears

pg I-10: I assume that capital sigmas, $\sum$, are missing in the two equations.

pg I-29: The habitat capability model must also be tested for sensitivity to roads and other human activities (Table 5). The factors in Table 5 are critical to the model and must not be ignored in the sensitivity analysis.

pg I-32: How were roads and other human activities, and how were habitat juxtaposition and interspersion incorporated into the computer model? I could not find them.

American Marten

See my general comments that address this habitat capability model specifically. This model requires considerably justification before it should be considered at all. The authors must demonstrate a good reason for not spending their time and effort testing Allen's model, which should be applicable to the Tongass National Forest.

pg J-3, para 1: The authors should cite Strickland's and Douglas' 1987 chapter in the book on Wild Furbearer Management and Conservation in North America edited by Novak, *et al.*, and published by the Ontario Ministry of Natural Resources and the Ontario Trappers Association.

pg J-3-4: Zielinski and Spencer showed that the diet of American martens they studied changed in a predictable manner through the seasons. During summer, the martens preyed on ground squirrels to some extent, sometimes heavily. The martens were most active during the day. When ground squirrels hibernated, the martens shifted to snowshoe hares and red squirrels and activity shifted to night. Red squirrels were captured mostly when sleeping in their middens. This sort of shift in prey should be incorporated into this model.

pg J-10, "Equations": This section says nothing about roads, yet roads are a critical aspect of the model. How are roads to be incorporated into the model? And why are roads not mentioned in this section at all?

pg J-11, Verification, para 2: This seems circular to me. The data from Chichagof Island were used to calibrate the model. Hence the model ought to make very good predictions for the island but the predictions are of little value because they are circular. One can not test a model with data used to develop the model.

J-30: Again, I do not see how roads and habitat juxtaposition and interspersion were incorporated into the computer model.

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River Otter

pg K-7, top: I do not see what is gained from converting all the linear measures to area measures. Habitat for otters is essentially linear; therefore, linear measures are most appropriate.

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Tongass National Forest
Land Management Plan

Scientific Review

by

John T. Ratti
Department of Fish & Wildlife Resources
University of Idaho

1. Background

I will not claim any intellectual background, but my basic philosophy as a member of a scientific review team is relatively simple. I feel we should state what we know and state what we do not know. I am critical of attempts to reach conclusions that are not strongly supported by good scientific research. Management plans must be based on science, but management must also be evaluated by science. Management without evaluation research is a waste of time and money...future management must be defendable. We must (at this level) act as biologists using critical honest thinking and remain relatively distant of political ramifications. At the present time, I find great comfort in recent guidelines announced by Jack Ward Thomas: "Tell the truth" and "Obey the law."

2. Comprehensive Review

A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska, Suring *et al.*, 1993, Review Draft

1. I initially reacted negatively to the "well-distributed" term in the title of this document (and as a basic objective for the process). Wildlife populations often have a clumped (aggregated) dispersion. Although I see little problem with using this terminology, especially for most of the species highlighted by this document, it might be best to note the "well-distributed" is intended to reference a dispersion pattern consistent with undisturbed populations.

2. Overall, the writing quality throughout this document is very good. Nearly all sections are clear and concise. I made a number of minor editorial suggestions on the manuscript., but in general I devoted little effort to such matters.

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3. On page 3 (and elsewhere), the National Forest Management Act definition of a viable population is quoted. Either a word or two is missing from the quote, or that is a very awkwardly constructed definition. As is, it states that an "existence is well distributed." Nonsense.

4. Throughout the document, there is reference to corridors to provide "linkages among HCAs." These are spelled out in some detail for some species accounts, and more vaguely for others. It was difficult to assess the impact of such corridors, since we did not have any mapped examples. Will all HCAs be connected by uninterrupted corridors or buffer strips? I feel this is an important issue that needs clarification before final assessment of the numbers, size, and distribution of HCAs can be made. In a letter to Ross Kiester, I have asked for an example map (restricted to a portion of Southeast, e.g., one island) that included all HCAs and other protected areas for review by the panel at the meeting in New Orleans.

5. I was a bit disturbed by items #2 and #4 of page 23, e.g., "to minimize the effect of HCAs on lands available for timber harvest." If I interpret this correctly, this is an attempt by biologists to appease the impact of sound biological decision making on economics, industry, and politics. This seems like game playing to me. We should simply assess lands that are protected and those that are potentially eligible for timber harvest. From the latter we propose proportional protection...period.

6. Throughout the document there is common reference to the timber harvest that will inevitably occur on the Tongass. One issue of importance with regard to assessing the adequacy of the proposed HCAs and corridors is the methods of future timber harvest. What will be the restrictions on clear-cut size? Will dead snags be left standing? What about edge type...abrupt vs. shelterwood cuts? Will travel corridors and patches of undisturbed forest be left within clear cuts?

7. Page 27; #3. Again, to access how reasonable the distance among HCAs is (i.e., "within the dispersal capability"), additional information on corridors and buffer strips is needed.

8. Page 30; "buffers at least 100 ft on each side of the stream..." Maybe I missed it, but seems like you will need a specific definition of stream, e.g., minimum stream flows (cfs) for a minimum number of months annually.

9. Page 30, Standards, #1. This statement concerns me; it implies weakness regarding the long-term status of any particular HCAs. For example, we all are fairly well aware of the Conservation Reserve Program (CRP), which was sold to Congress as a soil conservation effort, but also as permanent wildlife cover. Well, in many areas the permanent wildlife cover aspect has been a joke. Seems every year we have some type of emergency (e.g., drought, flooding) that

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allows the CRP ground to be hayed or grazed. I feel that this document should not provide an "avenue" for political pressure to shift an HCA to a less desirable site. **HCAs cannot be a moving target.**

10. Page 31, #2. I'm somewhat confused by reference to "second-growth forest" within HCAs that are primarily old-growth forest.

11. Page 31, #4. As with comment #9 above, I see some weakness and "open doors" with this standard. "Where other routing alternatives do not exist" is open to interpretation and the imagination (or lack thereof) and biases of the decision makers.

12. Page 32. I question the selection of Great Blue Heron as a species of Concern if fewer than 10 nesting locations have been reported ("ever") in Southeast. Obviously the region is very marginal habitat for this species and many factors (other than habitat) could negatively affect existing populations. Thus, we could easily interpret decreasing populations as a response to timber harvest, when in fact it could be some totally unrelated factor. Species distributions change. Because the vast majority of wildlife-habitat research has been conducted in optimal or high-density locations, we know very little about forces that influence species in marginal habitats.

Page 32, #2 under Goshawk. If you are using average home range estimate, then you have selected a habitat area that does not meet the needs of half of the population. Depending on the frequency distribution, you should select a home range that included 75-80% of the range of home range size from samples used to calculate the average.

13. Page 39, paragraph #2. "...provide the minimum habitat necessary to maintain a reasonably high likelihood of maintaining viable populations." How do you define "minimum habitat?" Is minimum the lower confidence limit of habitat needed for a viable population? If so, I do not feel that is biologically defensible.

14. Page 87, paragraph #1. Extinction is a natural process. We must protect species from becoming extinct due to anthropogenic factors, but we should not interfere with natural processes. For example, why are we managing habitat for Dusky Canada Geese on the Copper River Delta? Seems to me that the habitat changes, that have negatively affected recruitment, were the result of natural processes. Page 90, paragraph #2. Should read "large enough that they have little vulnerability to **man-induced** extinction processes."

15. Page 91, bottom paragraph. This is a weak review of "edge" concepts. Many new papers on this topic have appeared in the past 6-8 years, the issue is complex, and much more research is needed. In general, I found this paper (on

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conservation biology) a bit dogmatic with either biased or incomplete reviews of concepts.

16. Page 94, paragraph #2. Omit this paragraph on "endemic island species." Such species are almost always the result of founder populations and isolated adaptive radiation. Such populations ("especially for birds"), are usually far from continental margins. I fail to see how it is germane to this document. Does Southeast Alaska have one endemic island bird species? Other animals?

17. Page 101 (Great Blue Heron review). Palmer (1962) is a poor reference for subspecies classifications or distributions. For example, Palmer (1976) fails to recognize the subspecific status of the Vancouver Canada Goose, although data clearly indicate this population is geographically discrete and morphologically separable from other subspecies. All reference to avian species and subspecies (classifications and distributions) should be restricted to the American Ornithologists' Union Checklist of North American Birds (1957, 1983).

18. Page 144 (Boreal Owl). So few data are available on this species for Southeast, the value of the species as a MIS is limited with existing knowledge. This species (and others with poor local data) should be a high priority for future research

Appendix M. Fish and Wildlife: A Viability Risk Assessment

1. In general, this document is not very "reader friendly." I found many sections difficult to understand and confusing (especially the three analyses presented after page M-10). For example, in two consecutive paragraphs reference is made to "unproductive old-growth," "unharvested old-growth," "productive old-growth," and "unprotected old-growth." (I probably missed one!)

2. Page M-7. I was disappointed to find that most of the criteria (other than habitat and distribution) for selection of MIS species were abiotic. Have you considered a categorization of the MIS by some ecological criteria to see how they shake out, e.g., trophic level, symbiotic relationships, r- K- selection, etc. This may be a worthwhile exercise with regard to organismal balance.

3. Page M-11, Paragraph #2. I question the assumption that production old-growth is "the preferred habitat for old-growth associated wildlife species." For example, studies on Admiralty Island (Lebeda and Ratti, 1983) reported nesting and brood-rearing by Vancouver Canada geese on forest habitats classified by the U.S. Forest Service as poorly drained (F4 and F5). F4 soils have a Site Index (SI) rating of 120 for Sitka spruce (intermediate productivity), and F5 soils have an SI of 80 (no commercial timber due to excess moisture). I suspect that many other exceptions exist.

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Habitat Capability Models

1. After reading the first two chapters, and several species-model chapters, I feel moronic. I just don't get it. The text indicates that the "models are designed to assess impacts of change" in habitat condition. How? Will there be systematic sampling throughout the Tongass for each MIS to establish baseline values from application of the model? Will these sampling units be monitored periodically for input to the model to assess change? I assume my materials indicate this process somewhere, but I didn't find the methods spelled out.

On page ii-4, an example of "use of models for alternative comparison" is presented for marten. The example left me totally uninformed. Where did the numbers come from? Since no other document was cited, I assume the example should stand alone but it did not help me. These documents need one simple, clean, and clear example of model application from start to finish.

3. Species Reviews

Vancouver Canada goose (*Branta canadensis fulva*)

1. One major problem I see with the Vancouver Canada goose model is that "only habitat for nesting and brood rearing is evaluated in the model because, as indicated by Hanson (1962), this is probably the most limiting." I strongly disagree with embracement of this biological **opinion** regarding breeding habitat. At the time Hanson published this opinion, it was generally accepted by waterfowl ecologists that breeding habitat and factors affecting reproductive success were the critical limiting factors to overall population levels. This was largely due to the bias associated with available data; i.e., nearly all studies on waterfowl at that time had been conducted during the breeding season. It was not until 1981, when Heitmeyer and Fredrickson (Trans. N. Am. Wild. Nat. Resour. Conf. 46:44-57) published their pioneering paper on the influence of winter habitat on mallard recruitment, that waterfowl biologists shifted a significant portion of research effort to winter ecology. Since that time, winter ecology has become the central focus of many waterfowl research biologists (e.g., *Waterfowl in Winter*, edited by Weller, 1987, Univ. of Minnesota Press, 617 pp.; *Habitat management for migrating and wintering waterfowl in North America*, edited by Smith *et al.*, 1989, Texas Tech Univ. Press, 560 pp.). Waterfowl ecologists now recognize that for many cases winter habitat may be the most limiting factor affecting populations levels and recruitment (e.g., birds in poor body condition at the end of winter have less reproductive success than those in good body condition). **The main point is** that a good winter ecology study on *B. c. fulva* has not been conducted to date; i.e., we have no idea if breeding habitat is more limiting than wintering habitat. As a biologist with considerable experience with Vancouver Canada geese, I ***suspect*** that winter habitat (and

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winter survival factors) are much more limiting to this subspecies than breeding habitat. Winter stress factors for this population seem obvious and numerous to me, relative to limiting factors during the breeding period. A long-term and rigorous winter-ecology study should be a high priority for this MIS. The study referenced (on page A-3) that will "compile information on wintering areas" will be useful for such future research.

2. The habitat use review is very good and thorough. However, it should also note that the vast majority of the Admiralty Island nests located during the Lebeda and Ratti (1983) study were on Tiedeman Island (although overall nest-search effort was greater in habitats other than on this island). Tiedeman (maybe spelled Tideman?) is a small island in Seymour Canal, Admiralty Island. We never observed bear sign on this island, nor were we able to obtain records of observations of bear use of Tiedeman by biologists, local residents, and trappers. Thus, we speculated that bears may be important nest predators and concentration of nesting on this island was influenced by the absence of bears. More research on this topic is needed, and bear density may be an important factor to include in the HC model.

3. The use of *Vaccinium* spp. "as an indicator of cover density" seems appropriate. However are data available to indicate that this species of plant is directly related to overall vegetative cover?

4. In the model the DeMeo (1988) "index was assumed to be directly related to the amount of surface water available." Surface water is a critical issue. Was DeMeo asked if this assumption is reasonable?

5. Table 4. The source of the habitat categories (Table 4, column 1) was not clear to me.

6. I am not comfortable with assigning clear-cut stands a suitability index of 0. There has not been adequate research on this subspecies to justify this index value. I remember reports of a number of nests in a clear cut from the south portion of Southeast Alaska, but unfortunately I cannot locate the source (as I recall it was a one-summer survey by a woman technician).

7. Use of the estimated density of birds for one river drainage (Pavloff) seems unwarranted and will likely be a significant bias to model predictions. The USFWS (Juneau) has numerous years of waterfowl survey data that could be used to generate a more palatable estimate.

8. How will this model be used?

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Blue Grouse

(I was asked to read the Blue Grouse model also.)

1. I feel that classifying the Blue Grouse as "a major game species" in Southeast is a bit of an overstatement. I don't feel they rank as a "major" game species anywhere, and certainly not in Southeast where access to most habitats is very limited.

2. Based on the data presented in the model, the conclusion that "blue grouse do not respond positively to clear-cut harvest activities" in Southeast does not seem warranted.

3. With regard to calculation of grouse density, I am not comfortable with the assumption that nonbreeding yearling males (that do not hold territories) also do not hoot. For decades ornithologists made the assumption that calling or singing males represented nesting territory holders and provided an index to the breeding population. However, recent studies have disclosed a number of species where non-paired and non-territory holding males were actively singing, and thus inflated the estimate of the breeding population. Do we know for certain that silent males are never breeders? Has anyone contacted Fred Zwickle to ask his opinion on this matter and the assumption for the model?

4. Comprehensive Recommendations For The Future And General Comments

1. I feel that the process outlined by the three documents is a bit more complex than it needs to be.

2. A number of important assumptions are unwarranted or not supported by existing data.

3. Application of the habitat models is not clear.

4. The Viability Risk Assessment procedures need better organization and a more simplified presentation of procedures.

5. Stronger language is need for protection of the HCAs.

6. Much additional ecological research is needed ASAP on the Tongass to facilitate defensible application of this planning process.

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Tongass National Forest
Land Management Plan

Scientific Review

by

Mark L. Shaffer
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The Wilderness Society

1. Background

My academic background emphasized both vertebrate population ecology and land-use planning, but also included a broad range of biological and ecological topics. My Ph.D. dissertation research focused on defining and assessing minimum viable population sizes for the grizzly bear. This work involved developing extensive knowledge of statistical methods for data analysis, and computer modelling of vertebrate population dynamics.

My professional background has included teaching at both the graduate and undergraduate levels, additional research on population viability modelling, policy analysis related to land management and habitat conservation, and the administration of fish and wildlife research.

My basic philosophy most closely reflects the views and writings of Aldo Leopold and E.O. Wilson. I believe we live in a complex world that we barely understand and that without a basic respect for the great variety of life -- and our ignorance of it -- we could easily do ourselves harm. Science is our best method for increasing our understanding of the world we live in, but it is rarely sufficient to insulate our decisions from the necessity for judgement. Those judgements should be made with due caution.

The works that have most influenced my scientific views include Leopold's *Game Management*; MacArthur and Wilson's *The Theory of Island Biogeography*; Whittaker's works on plant community ecology; various monographs on particular species (e.g., Mech's book on wolves, Schaller's book on lions, etc.); and the works of Soulè on genetics and conservation biology. My conservation and planning perspectives have been most influenced by Leopold's *A Sand County Almanac*, McHarg's *Design with Nature*, and Wilson's *The Diversity of Life*.

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2. Comprehensive Review

This review is based on a complete reading of *Appendix M*, the general portions and selected species chapters (northern goshawk, boreal owl, gray wolf, and brown bear) of *Strategy*, and the brown bear chapter of *Models*.

Overview - Overall, I found this effort to be both encouraging and troubling. It is encouraging in the sense that it reflects an understanding of the scale and pattern of habitat that will be necessary for systematic conservation. It is troubling in the sense that it is superficial and implicitly accepts a paradigm of forest management that is not likely to be appropriate for this ecosystem.

The good features of this effort include a province-by-province approach; the recognition of the need for core areas, habitat corridors, and riparian buffer strips; the attempt at relative risk comparisons; and the provision of a map showing at least the coarse elements of the habitat pattern that would be conserved.

Bad features of the effort include accepting a permanent and fundamental alternation of natural disturbance regimes over much of the landscape; a number of apparently uncritical assumptions (e.g., that loss of 50% old-growth means high risk of viability concerns); a dissembling and schizophrenic rationalization of habitat capability models; failure to translate habitat numbers into population numbers; failure to visually portray or quantitatively analyze the full pattern of habitat that will result from application of the strategy; and the use of overly simplistic population models for assessing risk of extinction.

Rather than going point by point, I believe my review will be most useful if I explain my strategic concern and then outline what I believe would be an acceptable approach to this process.

Strategic Concern/Issue - My strategic concern is that this entire effort misses the point. On page 9 of the *Strategy*, it is pointed out that the forest ecosystem of the Tongass is "...typical of forests which develop in the absence of large-scale catastrophic disturbance." Blowdown is described as "...the most important natural disturbance process", and one that is a "...high-frequency, low intensity disturbance regime [that] typically affects individual trees or small patches of trees." The remainder of this entire exercise is then premised on forest management that has and will introduce a catastrophic management regime (e.g., clear-cutting) that is low-frequency and high intensity.

Moreover, this complete reversal of the natural dynamic will not be a one-time event. As stated on page 10, "Forest lands allocated to timber production are managed under a continuous 100-year rotation resulting in an essentially permanent change from the natural steady-state forest condition." This

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"permanent change" may eventually convert as much as 71% of the forest landscape in some provinces over the next 150 years.

Although there is certainly a legitimate place for the production of timber and other commodities from our national forests, I question whether the wholesale conversion of publicly owned landscapes for the provision of a single commodity is justified from either an economic, ecological, or public trust perspective.

Biodiversity is a public trust resource whose spectrum of values (environmental, ecological, utilitarian, humanitarian, aesthetic and spiritual) is increasingly recognized as a substantial -- even fundamental -- component of human welfare. Because the elements of biodiversity are unpriced in financial terms, our financial markets do not adequately allocate land for the maintenance of biodiversity. One major role of government in a free market democracy is to safeguard the public good from market failures. Thus, the allocation of public lands to maintaining the biodiversity public trust may, in a full macro-economic analysis, be the most rational use of these lands. This is especially true when we consider that current timber management on the national forests is heavily subsidized by the taxpayer.

In any event, the conversion of a large portion of the Tongass landscape to what will essentially be a tree farm makes the task of maintaining this ecosystem all the more difficult and places a premium on a thorough, systematic, and generous allocation of land to a natural habitat network.

A Suggested Approach to Habitat Conservation on the Tongass National Forest

Ecosystem Management - The Endangered Species Act of 1973 (ESA) requires, both implicitly and explicitly, that federal agencies conduct their activities in such a way as to prevent the endangerment of species, prevent harm to species already listed as threatened or endangered, and to assist in the recovery of listed species. In addition, the National Forest Management Act of 1976 requires the Forest Service to maintain viable populations of existing native and desired non-native vertebrate species on each national forest. Because all species are parts of some ecosystem, and because the loss, degradation, and fragmentation of natural ecosystems and the habitats they provide are the cause for listing most species, "ecosystem management" has been proposed as a more effective approach to fulfilling the intent of the ESA and NFMA than a species-by-species approach to habitat conservation. But what is ecosystem management?

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An ecosystem can be defined as:

> "...any unit that includes all of the organisms in a given area interacting with the physical environment so that a flow of energy leads to clearly defined trophic structure, biotic diversity and material cycles." (Odum, 1971)

Thus, management aimed at maintaining an ecosystem must provide for the continuation of the energy flow, trophic structure, biotic diversity, and material cycles that define each ecosystem. Because species are the "moving parts" of the ecosystem machine, if we maintain all the different species, then the energy flow, trophic structure, and material cycles should follow.

I suggest that, for the purposes of Forest Service Land Management Planning, ecosystem management be defined as the development and implementation of a specific plan of land allocation and management actions that:

1. maintains the full range of native plant communities in sufficient amounts and distributions to:

2. maintain viable populations of all native species, and

3. maintains the inherent productivity of the land as measured by meeting federal air and water quality standards forest-wide and maintaining per/unit primary productivity on those lands where the natural vegetation cover is altered via logging, grazing, mining, or other management activities.

If we accept this as a starting point, then the Wildlife Habitat Conservation Strategy becomes the Biodiversity Conservation Strategy portion of the overall Land Management Plan from an ecosystem perspective.

Developing the Biodiversity Conservation Strategy - The following is a skeletal outline of the steps and features of developing an overall Biodiversity Conservation Strategy for the Tongass National Forest.

1. Develop a GIS database incorporating available information on:

   a. geology
   b. soils
   c. topography
   d. hydrology
   e. vegetation -- to community type/seral stage
   f. special landscape features (caves, bogs, cliffs, etc.)
   g. anthro-features (ownership, towns, roads, etc.)

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Most of the physical information should be available at some scale from the U.S. Geological Survey, the Soil Conservation Service, or possibly state agencies. Both the vegetation and special landscape features are more problematic, but it is likely someone has proposed a vegetational community classification for Alaska. Start where you can.

2. From literature reviews, compile lists of species known or suspected of occurring in each community type/seral stage or in association with special landscape features. Draw on the State Natural Heritage Program and U.S. Fish and Wildlife Service Gap Analysis Program data and methods to assist in this step.

3. Conduct landscape analysis to determine what lands are reserved from resource development; the absolute and relative amount of each natural community type and special landscape features thus reserved; and the list of species thus included. To the extent possible, project abundance of species in reserved areas based on known habitat relationships and densities. Any species whose projected range of abundance falls at least partly below 5,000 individuals should be tagged as a potential viability concern.

4. Based on Step 3 above, select appropriate umbrella species for each natural community type and seral stage likely to be reduced in distribution and/or abundance under proposed management. Umbrella species should be a potential viability concern, require the particular community type/seral stage for which they will serve as an umbrella, and have among the lowest densities of species associated with that community.

5. For each umbrella species, develop a quantitative and spatially explicit population viability analysis model for assessing the impact of various patterns of land allocation on the risk of extinction.

6. Using these models, identify those land allocation/management alternatives that provide at least a 95% chance of each umbrella species surviving at least one natural regeneration cycle for the system in question (e.g., 200 years if it takes 200 years to regenerate the community.

7. Determine additional requirements for other species (e.g., Threatened/Endangered/Candidate, Management Indicator, or Sensitive) that may be of concern but do not qualify as umbrella species.

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Once the Biodiversity Conservation Strategy is developed, it can be combined with analyses of air quality, water quality, and net productivity requirements to identify those lands available for resource production. Once these steps are completed, the potential sustainable timber harvest can be estimated and an Allowable Sale Quantity set.

Real vs. Ideal - The current Wildlife Habitat Conservation Strategy parallels the above process only in the roughest form. Although some of the documents mention a GIS, I found no evidence of a comprehensive database that can readily portray to the scientist, the manager, or the citizen the variety, complexity, or repeating patterns that constitute the actual landscape of the Tongass National Forest. I found no attempt to fully describe the variety or composition of natural community types that make this landscape what it is. I found no attempt to systematically relate all known species to the different natural community types or to project their abundance through time as the proposed management affects this landscape.

The selection of species to focus on seems reasonable, but, wolves may be more of a viability concern than brown bear, given their much lower density and equal susceptibility to human-induced mortality. If wolf prey species find second-growth forest as unattractive as bears do, then this species could be in big trouble.

Finally, I found the quantitative population viability assessment for the brown bear too simplistic to give me much confidence. We know what the impacts of proposed management will mean for the survival of that species on this forest.

I know that the idealized process outlined above is a lot of work, and that there is considerable missing information and data that would prevent fully realizing the ideal at this time. But, I know the Forest Service can come a lot closer to that ideal than it so far has. And until the federal land management agencies begin to address the issue of conserving overall biodiversity at the level of technical sophistication that task requires, we will continue to see the federal government be one of the chief causes of species endangerment (Losos, 1993).

3. Species Review

None requested.

4. Comprehensive Recommendations for the Future

Taking the approach outlined above in Section 2 is the best recommendation I can provide for the future. Doing so will reveal and help

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prioritize which of our gaps in knowledge or data are most important to fill and thus help to structure both the research and monitoring agendas.

5. Species Specific Recommendations for the Future

Although none was requested, I believe that very realistic models of both brown bear and wolf meta-population dynamics could be constructed based on a composite of knowledge and data on these species from many different areas. This would provide a far better assessment of their likely viability under different management scenarios than the current work provides. Such models would also provide the hypotheses necessary to structure an effective and efficient monitoring program.

6. Other Comments

I want to underscore that my overall assessment of the current effort is mixed. If the decision is made to convert much of the Tongass landscape to 100-year rotation timber stands, then I think the strategy is on the right track, but that much work remains to be done to demonstrate that it is sufficient to maintain the overall biodiversity resources of the Southeast Alaska ecosystem. The net effect of my concerns is that this strategy may not go far enough, thus risking failure to comply with both NFMA and ESA.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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Kansas State University

1. Background

My professional background started in graduate school as part of a closely knit group of graduate students whose interests were in evolutionary ecology. The group included Mary Willson, Eric Pianka, Jerry Verner, Henry Horn, Lowell Spring, and Tom Frazetta. The faculty that led and stimulated this group were my major professor, Gordon Orians (evolutionary ecology), Bob Paine (community energetics), and Richard Snyder (vertebrate functional anatomy). Since graduate school, the colleague who has had the most influence on my thinking is Steve Fretwell. Our frequent disagreements forced me to rethink my ideas and to integrate the regulation of population density into my ideas on the evolution of the structure of nature.

In approaching biological issues, I ask what types of selective pressures are likely to have structured the biology of the group of species I am studying. Using the speculative answers I give to those questions as working hypotheses, I measure aspects of the anatomy, physiology, or behavior of those species to determine if they fit my hypotheses. Because it is difficult to imagine all the factors that impinge on the evolution of one simple trait, I often find myself adjusting the details of my hypotheses after the initial measurements, thus reversing the accepted hypothetical-deductive approach to science. Because nature is not simple, I try to build a consistent world view involving patterns of cause and effect so that when observations contradict that complex world view, I can pay particular attention to those details and check their validity and the validity of my world view.

I find David Tilman's models of trade-offs in resource-based competition the most helpful in integrating the regulation of the population density with the evolution of competing species. I also like Bruce Wallace's use of ecological competition to explain how overdominance at many loci may still be compatible with a reasonable genetic load. I think that the greatest theoretical problem facing field biology is integrating population genetics with population density

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regulation as the causal basis for the patterns described by community and ecosystem ecologists.

2. Comprehensive Review

Each of the three documents seems internally consistent, but the dates on the different documents make it unclear how they were developed as part of an integrated plan to maintain viable populations of wildlife. "*A Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska*" (hereafter referred to as "*Strategy*") has the most recent date (May 1993). It gives the foundation for which species of birds and mammals deserve the most concern over possible extinction and the management plan to avoid population loss in those and all other species. The second document ("*Appendix M*") is dated February 1992. It gives criteria for choosing Management Indicator Species (MIS) which are to be used to monitor the effectiveness of the plan to maintain viable wildlife populations. I would expect the choice of MIS to rely, at least in part, on *Strategy*, but that does not seem to be the case. *Appendix M* has as its main function the assessment of viability risk for wildlife populations based on what fraction of the old-growth timber will be cut in 21 different ecological provinces and what fraction of the Habitat Conservation Areas (HCA) will remain unaffected in each of the 21 provinces. The third document (hereafter called "*Models*") contains 14 habitat capability models for the final 13 MIS chosen in *Appendix M* plus the blue grouse. These models are dated either 1988 or 1992 which predate *Appendix M*. However, *Appendix M* does state that the final MIS were chosen in 1988.

The criteria used for evaluating the viability of populations in *Strategy* seemed to be redundant at first reading. For example, 6. (potential exists for inbreeding depression), 7. (high potential exists for local extirpation), and 8. (capability to disperse is limited or barriers to dispersal exist) all seemed to indicate small isolated populations. However, when I checked the use of these three criteria on a variety of species in table 2C and 4C, they showed reasonable independence. The listing of species in tables 1C-4C seemed consistent with my understanding of the species, sketchy as that is. The species accounts and conservation strategies seemed reasonable. An analysis of the literature cited for three of these species accounts that I picked at random showed that 87% of 156 references were dated 1980 or later. I am impressed by the organization and thoroughness of *Strategy*.

Appendix M gives the criteria for choosing MIS, but it does not go through a detailed procedure, equivalent to the evaluation of population viability in *Strategy*. Only 5 of the 9 species evaluated as giving the greatest concern for viability in *Strategy* are included as MIS in *Appendix M*. River otters are added to the original 12 MIS to make 13 MIS. Of the 13 MIS, only hairy woodpecker, red-breasted sapsuckers, and brown creepers are species that are not hunted,

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trapped, or of great interested to the public. The general basis of choosing species is heavily weighted towards general public interest rather than how modification of habitat through logging will endanger the viability of bird and mammal species. All three of the nongame species listed above are trunk gleaners, while no twig or needle-gleaning species of birds are listed. A more detailed justification of the 13 MIS species would be a big help in evaluating whether viability risk assessment for all species will be accomplished by studies of the 13 MIS.

A major part of *Appendix M* is viability risk assessment based on what percentage of HCAs will be affected by timber harvest in each ecological province and what part of productive old-growth timber will remain in the years 2000, 2010, and 2140. The years 2000 and 2010 are used because that is when long-term sale contracts for lumber end. There may be some justification for logging in HCAs if contracts specify some part of some HCAs, the Forest Service has no legal grounds for changing contracts, and there was no better place for the HCAs. I do not understand, however, why on the top of page 31 in *Strategy* it states that, "Harvesting of existing second-growth forests may be permitted within designated HCAs that fully meet the habitat composition criteria.....". What seems even more destructive of the HCA concept is that between 2010 and 2140 under any of the five patterns of land use a major fraction of the HCAs in most ecological provinces will experience some logging. Why set aside HCAs if they are not to be maintained? Existing logging contracts can not be blamed for these types of manipulation of habitat within the HCAs. The justification of this land use is necessary if *Appendix M* is to be taken seriously, or for that matter, any of the documents are worth the effort put into them.

Models contains Habitat Capability Models (HCM) for the 13 MIS, and in addition, blue grouse. The models use existing literature to estimate the relative population density of each MIS in the different habitats of the Tongass National Forests. A Geographic Information System (GIS) being developed for the Tongass National Forest will then be used to estimate the area covered by the different habitats. The population trends can then be estimated by summing the products of habitat area times the relative population density for that habitat for the GISs at two different times. I can not read the programs for the models, but no mention of spacing of HCAs and their effect on population viability seems to be incorporated into the discussion of the models. The logic of *Strategy* and the integrity of the HCAs seems to be critical for the HCMs. The strength of the HCMs is dependent on understanding the effect of different habitats on the population density and resilience of each of the MISs. The analysis for marten in *Models* was authored by Suring and others, while for *Strategy* it was done by Flynn. Suring cited 72 references (40 from 1980 and after) while Flynn cited 58 (50 from 1980 and after). Many of the earlier references cited by Suring concerned diet and seem appropriate in analyzing the relative merits of different habitats. The HCMs seem to be thorough and creditable efforts. I hope that future work by the wildlife personnel will be field testing of the generalities made about the relative values of different habitats to the MISs.

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3. Species Review: Red Squirrel (*Tamiasciurus hudsonicus*)

The Habitat Capability Model (HCM) for red squirrels in the Tongass National Forest is reasonable for years in which Sitka spruce and western hemlock have average or better cone crops, but may be far off when a cone failure follows a below average year. During cone failures, squirrel populations in damp coastal forests of Washington and British Columbia move out of mature forests into alder and maple trees along streams and into lodgepole pine forests on very rocky areas (personal observation). These were the only forests producing a seed crop. The same behavior could occur in the Tongass National Forest. Ruth and Berntsen (1955) show that western hemlock and Sitka spruce both had crop failures in the same year as Garman (1951, 1955) showed for other conifers which mature seeds during the same growing season in which they are pollinated in damp coastal forests. It would appear that these tree species all have individual trees cuing off the same environmental factors to vary the number of cone buds between years. Buds in conifers can become vegetative shoots or cones depending on hormonal balances (Allen and Owens, 1972). Thus, the flowering of trees in the damp coastal forests can cue off broad ranging weather fronts and vary in phase over a broad area. Varying flower production in phase between trees of the same wind-pollinated species can increase the frequency of pollination and the efficiency of seed production (Smith *et al.*, 1990). By different species of conifers cuing their flower and seed production off the same weather variables, they can cause regional food failure for seed-eating animals over broad regions (Janzen, 1971; Smith, 1970; Smith and Balda, 1970). The fact that the subspecies of red and Douglas squirrels found in the damp coastal forests are much smaller than the subspecies in the drier interior forests is indicative of the coastal species experiencing low food supply more often. As in the Tongass National Forest, most coastal forests do not burn and thus had continuous old-growth forests before the advent of the logging industry. Coastal forest would have very little alternative habitat for squirrels to enter during a cone crop failure. In the interior forests, serotinous lodgepole pine, which provides a constant though difficult food supply, is available in areas that are frequently burned. The seeds of Sitka spruce and western hemlock are relatively small compared to the seeds of interior trees as would be expected for the damp germination sites of coastal forests (Baker, 1972). The rarer conifers of the Tongass (mountain hemlock, western red cedar, and Alaska cedar) also have small seeds. Moreover, all species except Sitka spruce have relatively few seeds per cone. Thus, when squirrels carry one cone at a time to cache, they are caching food at a much slower rate than squirrels of interior forests. All the above considerations should lead to selective pressures for small squirrels whose populations fluctuate fairly drastically with the size of cone crops in Sitka spruce and western hemlock.

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The use of red squirrels as an MIS is a very good idea because they are diurnal and fairly vocal. In addition, they repeatedly cache conifer cones in the same midden over many years. Thus population trends over several years can be measured by looking for activity on a series of middens each year. Crossbills, siskins, shrews, red-backed voles, and deer mice all use conifer seeds as a large fraction of their diet when the seeds are abundant in coastal forest, but have different responses to cone crop failures (Smith and Balda, 1979). The annual pattern of variation in squirrel populations should be dependent on the annual variation in conifer seed crops and should also mirror the variation in populations of other animals that us conifer seeds as a large part of their diet. Goshawks and marten use red squirrels as a significant part of their diet and might have population trends that mirror the annual variation in red squirrel populations. This is more likely for goshawks which are strictly diurnal like red squirrels.

In much of their range, red squirrels respond to cone failures by emigration (Smith, 1968). They have been reported to swim large lakes in the process. It is interesting that squirrel populations were not found on most of the large islands of the Tongass. It is likely that the cold northern marine currents in the area would cause hypothermia before the squirrels could swim very far. The surface of northern lakes may warm considerably by late summer when squirrels often emigrate. If the old-growth coastal forests are relatively uniform, then the squirrels of the Tongass may not have gained by emigration, but rather were better off by substituting caches of dried fungi for conifer cones. It will be interesting to observe the behavior of squirrels to cone failures. If alder or birch are common in early successional stages after clear-cutting, then squirrels may immigrate to logged areas when there are cone failures in the old-growth forests.

4. Comprehensive Recommendations for the Future

4.1 Philosophical and Conceptual Considerations

I would like to have the basis of choice of MIS spelled out in detail. The present choices seem to have the Forest Service doing the job of the Alaska Fish and Game Department in monitoring the populations of game species or fur bearers. If the road making that goes with logging brings in so many trappers that the populations of fur bearers are endangered, then it would be good to go to the Canadian system of registering trap lines to specific trappers. Under that system, individual trappers will be more likely to trap just enough to maintain the populations at a steady state in their exclusive areas. The Forest Service should commit itself to eliminate logging on the HCAs. Otherwise, there will be continual pressure to log more of the HCAs as old-growth stands become rarer. I did not notice a definition of what size stream should warrant having a 100-foot zone of uncut old-growth timber on each side of it. That rule should be made.

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4.2 Program of Research

Of all the species in the Tongass, northern flying squirrels should be most endangered by the patchwork of clear-cut areas because it is relatively helpless on the ground. It would be particularly important to find out if they used the 200-foot wide bands of forests along streams and the 500-foot wide bands of forests along the coast. If they do not, then the present system would be lethal to at least one species. The problem is that northern flying squirrels are difficult to work with. They eat fungi and arboreal foliose lichens (McKeever, 1960 and Maser *et al.*, 1978) so that their populations probably will not vary in phase with red squirrels.

4.3 Program of Monitoring

For the monitoring program to be meaningful there should be a control to which the changes in the Tongass could be compared. It would be good to have large HCAs that will be having logging beside them in the near future, others that will be having logging beside them in the distant future, and equivalent areas in Glacier Bay National Park that will never be logged to see the effect of logging on nearby HCAs. The most obvious thing to monitor is population density. Questions about effective gene flow and the importance of subdivisions of populations being isolated on HCAs would require measurement of genetic variation in the populations.

5. Species Specific Recommendations for the Future

The red squirrel is an ideal MIS because its diurnal, vocal, and caching behavior make it easy to census. It is dependent on conifer seeds for a large part of its diet and its population fluctuates with the abundance of the annual conifer seed crops. It is a good species to use as an indicator species for population variation in other seed eating mammals and birds.

The northern flying squirrel is a difficult species to study because it is quiet, nocturnal, and has a food supply that is difficult to quantify. By eating lichens and fungi in the old-growth canopy, northern flying squirrels are the closest thing to an arboreal grazer in the boreal forest. Their size and potential productivity make them an important prey to marten. Since marten and goshawks are two of the species of greatest concern in *Strategy*, it would be important to study the interaction between red squirrels and flying squirrels as prey and goshawks and marten as predators. Because red and flying squirrel populations have not made it to some of the larger islands in the Tongass, it should be possible to use uncolonized islands as controls in the interaction

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between the above predator and prey species. Do predator populations remain at a lower and more constant density on islands without red and flying squirrels?

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Tongass National Forest
Land Management Plan

Scientific Review

by

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1. Background

As a wildlife researcher and professor on forestry faculties (UC Berkeley, UM Missoula, UW Seattle) I have been involved with forest/wildlife relations for over 40 years, locally, nationally, and internationally, as detailed in my C.V. As international interest in wildlife conservation has grown, I have contributed to the International Union of Forestry Research Organizations (IUFRO) and to the International Union for the Conservation of Nature and Natural Resources (IUCN). IUCN, along with the World Wildlife Fund, and the United Nations Environmental Programme, recognizes that the major cause of renewable resource loss worldwide is liquidation, the speedy exploitation of valuable, vulnerable species of plants of animals for maximum short-term profit. They have therefore adopted the philosophy of sustainability, as developed in *Caring for the Earth: A Strategy for Sustainable Living* (IUCN/UNEP/WWF 1991, Gland Switzerland).

As an aid in implementing this strategy, various working groups have been appointed by IUCN. One of these, on which I serve, has recently produced *Guidelines for the Ecological Sustainability of Nonconsumptive and Consumptive Uses of Wild Species*, which will be submitted by the IUCN Director General for approval by the IUCN General Assembly in January 1994.

With regard to wildlife conservation, specifically, IUFRO has conceived it to have three principal goals:

1. The sustained perpetuation of gene pools.
2. The sustained use of wildlife by humans.
3. The alleviation of friction between wildlife and other human values.

My own philosophy, which you request, is in line with the foregoing. I would add an emphasis on the necessity, in wildlife conservation, of encouraging

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the active cooperation and participation of the local people, the people who have continual interaction with wildlife habitat and populations.

This philosophy is not too different from that of Gifford Pinchot, with his emphasis on the sustainability of multiple forest uses, and his recognition that without support by the local people the program could not succeed. In modern days the concerned public includes much more than the local people, so the "public interest" speaks with more than one voice and they all should be considered.

2. Comprehensive Review

To attain, and maintain sustainable use requires the relevant basic knowledge concerning the resources involved, and the successful application of that knowledge in increasingly complex human cultures. At various times in the past sustainable use of forests and forest wildlife has been successfully maintained with rule-of-thumb knowledge and overwhelming police power. In industrialized nations overwhelming police power is generally not acceptable. The alternative is cooperative acceptance of a recognized public interest. From the early 1900's to around 1960-70, the recognized U.S. public interest in wildlife was largely utilitarian: to encourage game species and control their predators. Since then the recognized public interest has broadened to cover the welfare of all wild species.

When the recognized public interest was utilitarian, the Forest Service could successfully engage the cooperation of state and federal agencies in population management of game and large predators. When the recognized public interest broadened to include all wild species, most of which are neither game nor large predators, the task of wildlife conservation largely returned to the public land management agencies.

The problems involved in integrating wildlife conservation with timber harvesting are formidable, both with regard to a lack of basic information, and adequate development of successful integration of new wildlife conservation goals with traditional timber management programs.

While various USFS directives have indicated that wildlife should be "considered" with other resources in managerial plans, it was not until the Endangered Species legislation that any wild species was put in a preeminent position with regard to planning priorities. This naturally focused managerial attention on species which might soon move into the endangered category, and particularly on possibilities that this might be avoided (e.g., Thomas *et al.*, 1990, 1993).

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An overlapping mandate has been the directive to sustain biodiversity, interpreted as native and those introduced species which are desirable to maintain.

In addressing these directives forest planners have proposed to maintain "minimum viable populations", which are populations maintained at the lowest level that will still survive indefinitely in the years ahead.

These concerns drive the material under review. There are two main themes in these documents: the conservation of the entire natural biota (and favored introductions) through perpetuation of adequate habitat, and the specific relations of selected wildlife species to habitat factors, partly expressed in modelling. The potential significant themes not developed in these documents, which include biological feedback, integration with local cultures, and effective input to all managerial programs, are discussed under (4): Comprehensive Recommendations for the Future.

The themes of habitat perpetuation, and wildlife population modelling, are useful and important first steps toward an ultimate effective system of forest-wildlife integration. The habitat pattern proposed in these documents appears to be well-founded. The modelling effort is hampered by a shortage of information, both in basic biology and the ways that population biology is affected by habitat change.

As Suring (1993) notes, models provide a rapid and consistent evaluation of habitats and management effects. That is, the model is a relatively simple calculating machine that manipulates variables consistently in accordance with its design. It conveys a sense of precision. What it, in its static form, does not do may be illustrated by reference to a rifle and its uses. Each rifle and load acts with a certain level of precision, as reflected in the span of a well-aimed group of shots. This is useful but not sufficient. For sufficiency the shots from the rifle must hit the target. That is accuracy. A model can be trusted to be accurate only after its predictions have been tested against reality and, when "off the target", adjusted to increase accuracy. This is not to deny that models are great aids in thinking about how various factors interact. But they can be highly misleading if their attractive precision is mistaken for accuracy.

3. Species Review

Not requested.

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4. Comprehensive Recommendations for the Future

4.1 Philosophical and Conceptual Considerations

Over the past five decades, wildlife populations have been assessed by various kinds of census or, more commonly, index to levels and trends. Correlation with habitat structure and change has been attempted, often successfully, but usually only with regard to one or a few species. In any particular study it has been common for a priori assumptions to be quickly discarded as actual facts accumulate. Similarly, ideas about just what evidence should be obtained to shed light on a significant problem are frequently modified as what data can really be obtained becomes clearer. For a particular region, field study in that region is necessary for a clear understanding of species-habitat relationships.

Wildlife populations vary seasonally and from year to year, in the same habitat, but some direct measure of relative population size or density can generally be made.

However, it cannot be denied that the gathering of wildlife population data is labor-intensive. When costs must be kept down, which is generally the case, substitutes can be devised. One in common use is to replace quantitative population values with quantitative potential habitat values. It is easier to measure selected habitat factors than wildlife populations, and therefore more practicable and convenient.

At the same time, the assumptions of potential habitat values suffer the weakness of all assumptions - they are not dependable unless they are tested and corrected by reference to reality. In the days when the focus of interest was on huntable game populations, it could be argued that hunting pressure might lower populations below the "carrying capacity" of the habitat so that a direct population estimate was too low to reflect habitat capability. The current broader interest in all wildlife species includes a majority which are not hunted so their populations reflect habitat capability (interacting with weather, etc.) more directly.

Emphasis on assumed potential habitat values for a species tends to neglect what a species can show in its movements or in its physical attributes concerning the quality of its habitat. For example, if the species must search for food more widely or actively in one habitat than another, that fact can be ascertained by routine radio-tracking of representative individuals. This immediately directs attention to the difference between habitats. This may be correlated with already-recorded habitat attributes or, more probably, lead to a closer look at how the habitats differ. If there are no closer looks the whole process will fail in the long run, because not everything can be taken into consideration at the beginning. In other words, a conservation plan for forest

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wildlife must include periodic monitoring, reassessment of relationships on the basis of monitoring, and incorporation of new information in the management plan.

The development and application of Geographic Information Systems (GIS) has vastly increased access to habitat information. But people who develop such systems cannot a priori cover every possible factor. Therefore wildlife field studies may potentially raise questions that require modification of the GIS for their answer.

There appear to be two approaches to wildlife habitat quality questions: to construct the model from present understanding and test it against reality, or to monitor wildlife populations and habitats and model the relationships discovered. So stated, the differences are reduced to zero since both models and monitoring are necessary for development of accurate assessments.

If continued monitoring of wildlife populations is necessary for the development of accurate models, there should presumably be a more specific monitoring program spelled out in the wildlife conservation plan.

The concept of "minimal sustained viability", emphasized in these documents, is relevant for species that might be threatened with endangerment, species of great concern to forest management in these days of the Spotted Owl. This concern must be expressed in managerial planning. At the same time, however, species not apparently in danger, and in fact reasonably abundant, are useful as potential habitat indicators and, in some cases, important for local people.

Fourteen species are covered in the present report on *Wildlife Capability Models for Wildlife in Southeast Alaska* (Suring, 1993): Vancouver Canada Goose, Bald Eagle, Blue Grouse, Hairy Woodpecker, Red-breasted Sapsucker, Brown Creeper, Gray Wolf, Black Bear, Brown Bear, Marten, River Otter, Sitka Black-tailed Deer, Mountain Goat and Red Squirrel. In the *Proposed Strategy for Maintaining Well-distributed, Viable Populations of Wildlife Associated with Old-growth Forests in Southeast Alaska* (Suring *et al.*, 1993) there is an overlapping, but different list, identified as "potentially most sensitive to modification of old-growth forest in southeast Alaska". The eight species listed are Great Blue Heron, Northern Goshawk, Gray Wolf, Brown Bear, Marten, River Otter, Mountain Goat, and Northern Flying Squirrel.

This second list responds to continental public concern, expressed in Endangered Species legislation with the potential for imposing enormous constraints on the options for land management. It does not respond in an obvious way to local public concern and interest. Yet local people, through local political pressures and through their daily behavior in wildlife habitat, can perform as loose cannons if their immediate interests are not prominently

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included in the management program. From this perspective it would seem wise to enlarge the wildlife conservation program in a formal way to include all game species.

In addition, it would seem to make sense both culturally and economically to integrate upland, riparian, and fresh water into a salmon conservation and management program.

Emphasizing the importance of game and fish to the local people helps focus attention on the whole forest and its environment. Although there is a current necessary focus on old-growth forest and its importance in maintaining many species, it is well to consider that whatever pattern of natural old-growth forest is established will exist in a landscape that includes production forests and other sorts of habitats. Access to these via road and boat brings local people, and their behavior with regard to wildlife affects the conservation of some species. If local people do not cooperate in the conservation of readily seen species (the wolf, brown bear and bald eagle are obvious examples), then those species may well suffer population decline no matter how well old-growth is protected.

Emphasis on a relatively small list of species associated with old- growth forests (Suring *et al.*, 1993) also neglects the opportunity to gain ecological knowledge from species that are common and easy to monitor. When a well-designed monitoring program is integrated with a relevant GIS, much new information concerning habitat relationships can be found.

4.2 Program of Research and 4.3 Program of Monitoring

There has traditionally been a separation of Research and Management in the National Forest System. This has led some managers who routinely cruise timber to relegate wildlife mensuration to Research and therefore not in their managerial program. In reality, the line between research and mensuration does not exist. Research requires data, for which mensuration is necessary. It would help resolve ambiguity if research and monitoring were combined as mensuration and analysis. The questions for which analysis seeks answers will vary over time. If mensuration is well designed and conducted, its results can be analyzed in different ways as new questions arise. Mensuration comes first. It tells what is on the ground, and how it varies from place to place and time to time. A good current example is the April 1, 1993 initiative for each Region to prepare and submit a Regional plan for monitoring neotropical migratory birds. Such a plan, well-designed and fully implemented, can mesh well with GIS to shed light on many habitat relationships. Such a system will monitor many wildlife species in addition to neotropical birds at little extra cost (Dobkin, 1993; Manley *et al.*, 1993; Paige, 1993).

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Mensuration of game and fur-bearing species has long been carried on by state and other entities. Integration of these efforts with variation in southeast Alaska habitat and time can provide a base for ecological analysis, as shown by the relatively rich store of data used in the models of Brown Bear and Sitka Black-tailed Deer populations under review.

Mensuration of additional species can serve to fill data gaps, according to need. And mensuration can include much more than enumeration, as variations in physical condition, reproductive rate, home range size and diet, among others are correlated with variation in habitat, season, and year.

Information flowing from a system of mensuration and analysis can affect the evolution of forest management plans and programs, and vice versa. Much progress has been made recently in advancing the concept of Ecosystem Management toward actual application on public lands (e.g., Jensen and Bourgeron, 1993). Wildlife conservation programs that include habitat management obviously fit well into Ecosystem Management, but actual implementation will require the evolution of new ways of thinking and doing, an evolution in which research and monitoring will play a part.

5. Species Specific Recommendations for the Future

Summarizing some of the foregoing, the following groups of species should all be prominent in the plan:

1. Old-growth associated species.
2. Of significant economic or cultural importance.
3. Readily monitored and associated with habitat variables.

6. Other Comments

The authors of these reports should be complimented on their emphasis on the major consequence of public land management practices, loss of old-growth forest and its associated biota. Their methodology and conclusions appear to be well conceived.

What more might be done if time and resources were available is no doubt as obvious to them as to your reviewers. Other regions have moved ahead more rapidly toward a broader concept of public land management, and the resolution of problems that consequently arise (e.g., Thomas *et al.*, 1993) and much thought has been given to how this could fit into land management planning (e.g., Jensen and Bourgeron, 1993; Christensen *et al.*, 1993). Some of these will no doubt be found applicable to the Tongass.

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Tongass National Forest
Land Management Plan

Scientific Review

by

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1. Background

I was trained as a behavioral ecologist, and much of my research has focused on the ecological basis and evolution of avian behavior. My thinking about evolution has been greatly influenced by the ideas of Arnold, Lande and Wade (Arnold and Wade, 1984a, 1984b; Lande, 1976, 1979; Wade, 1980) due to my connection to the University of Chicago. Because of this I have always had an active interest in population structure and population dynamics. My views about population biology are otherwise traditional, being rooted in the paradigm of density-dependent regulation (e.g., Caughley, 1977). Thus, in cases of population decline I attempt to distinguish those due to changes in carrying capacity from those due to changes in demographic parameters independent of carrying capacity. The decline of the red-cockaded woodpecker (*Picoides borealis*), a species I have studied extensively, I view as the former; the decline of pelicans and raptors due to egg-shell thinning and extinctions of island forms due to introduced predators I view as the latter. I also view effects of habitat fragmentation as the latter, and define them as reductions in abundance in fragmented landscapes above and beyond those attributable to reduction of carrying capacity through habitat loss and degradation.

My work on the endangered red-cockaded woodpecker and an interest in habitat fragmentation have propelled me into the field of conservation biology in recent years. I consider my contributions to conservation biology to represent applied behavioral ecology. My focus remains on the ecological basis of selective pressures on behavioral traits, and consequences for population biology. To this I add in recent work exploring implications for management and conservation. An important recent addition to my conceptual framework is metapopulation dynamics (Pulliam, 1988; Harrison *et al.*, 1988). I find this as attractive a paradigm for thinking about how groups of conspecifics in different habitat patches interact as density-dependent regulation is for thinking about how conspecifics in the same patch interact.

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My interest in conservation biology is strongly grounded in my personal philosophy. I have long had an interest in and empathy for wildlife. Equally importantly, as a scientist I firmly believe that many, although not all, aspects of ecological theory have matured to the point that they can be applied successfully to natural resource problems. I believe that advances in relevant basic biology are the key to advances in management, and that these advances depend on rigorous application of the scientific method. I further believe that quality science can be done in the field, and that there is little reason to be satisfied with less in this day and age. I am fond of field experiments and replication, and distrustful of correlations and expert opinions. My convictions have been validated by my own success in following this approach in studying red-cockaded woodpeckers. My colleagues and I conducted a field experiment to test a hypothesis about the evolution of species' cooperative breeding system (Walters *et al.*, 1992), the results of which led to a new understanding of population dynamics that formed the basis of a new management strategy (Walters, 1991) that has been quite successful. I realize that management decisions must be made before all relevant scientific questions are answered, but management philosophy and scientific inquiry should be integrated and evolve together, regardless of the issue.

2. Comprehensive Review

The relationships between the three documents reviewed were not explicitly stated. My evaluation of these relationships is that the "*Strategy*" document represents the procedure to be used to maintain well distributed populations of all vertebrate species. The "*Risk Assessment*" is an attempt to estimate the effectiveness of this management strategy. The "*Habitat Capability Models*" can be used as a safeguard to determine whether the management strategy indeed provides for all elements of the community, and not just the eight species whose biology was considered in developing the strategy. The models project populations of representative species that serve as indicators of various elements of the animal community.

I will begin my review with the "*Strategy*" document since it is the heart of the management plan. I think the approach taken, which is to identify vertebrate species most sensitive to change in old-growth forest, and combine the most restrictive elements derived from species-specific management to produce an overall management strategy that considers landscape level features, is excellent. The approach is well-grounded in the best current information in conservation biology, and therefore can be successfully defended. The specifics of the strategy, that is, the results derived from this approach, are not so easily defended. This is a direct result of a general lack of relevant scientific information. Often estimates of key parameters are little better than guesses, or are derived using a series of questionable assumptions from very indirect measures. It will be easy for someone to claim that details of the strategy are likely incorrect, but impossible for someone to say how those details should be

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changed. Therefore the most critical need in evaluating the proposed plan is to determine how much difference it makes how incorrect the parameter values used are. Does the proposed number and arrangement of HCAs result in population levels near those desired even if parameter values such as the frequency of movement between HCAs certain distances apart, the number of individuals expected to inhabit an HCA of a certain size, and the number of individuals required to ensure demes are reasonably stable, turn out to be incorrect?

One aspect of the approach that can be questioned is the inclusion of non-biological considerations in developing the details of the strategy. Normally these types of planning efforts consider only the relevant biology. Concessions to factors other than biology are then made through modification of the original plan. Concessions to timber harvest and hunting have already been made in this plan. Therefore one cannot be as flexible about making concessions through plan modifications as one otherwise might be, or the biology will be overly compromised.

The greatest concession to nonbiological factors is that it is assumed that the landscape of the future will be a network of HCAs interspersed with large clear-cuts of various ages. No justification is given as to why this is the desired landscape, as opposed to others characterized by more, much smaller gaps. I find it surprising that the biological consequences of alternative methods of forestry are not discussed. Surely the reasons for selecting the landscape chosen are not biological. Alternative landscapes more favorable to wildlife should be proposed as options and justified on biological grounds, and it should be made clear that the landscape depicted in the current plan can only be justified as desirable based on timber harvest, not wildlife conservation, objectives.

It might be helpful to portray habitat modification through timbering in terms of microhabitats that exist in the ecosystem. Regardless of impacting process, habitat does not disappear, but is converted to another type. This process favors some species at the expense of others. Even in the extreme case of a forest being cleared for urban development, pigeons and house sparrows benefit, albeit at the expense of a much larger number of species. What do clear-cuts and the resulting regenerating forests represent in this system? Are they totally foreign to the system and thus of little use to any local species, or do they function as large tree-fall gaps, favoring that subset of species that make use of the various successional stages created by a tree-fall? If timbering practices were altered, for example to uneven-aged management or some other technique that would result in smaller cleared areas, would cutting mimic tree-falls more closely, and thus have less impact on the community?

Although an emphasis on old-growth forest is appropriate, it need not be to the exclusion of other habitats in the Tongass. It would be useful to indicate how changes expected under the management plan are projected to affect the

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abundance of other habitats, as well as various microhabitats within old-growth forest, and thus species dependent on these other habitats and microhabitats. Perhaps this information is provided in documents other than those I reviewed. Based on what I reviewed, I perceive a major need for studies that document habitat and microhabitat relationships of the species found within the Tongass. This has been done for individual species in some cases, but what is needed is community-level, not species-level, sampling. This is easily accomplished, for birds, at least, through point count censusing. To interpret density data (Van Horne, 1983) it would be useful to obtain data on nesting success in critical habitats and microhabitats as well (Martin and Geupel, in press).

My biggest criticism of the specifics of the conservation strategy is of the mechanism used to identify sensitive species. Factors related to issues currently topical in conservation biology were weighted too heavily (criteria 5, 6, 8) and factors more firmly grounded in basic ecological criteria were not weighted heavily enough (10, 11, 13, 14, 15, 16, 17). The criteria reflect a provincial approach. A widespread, abundant species on the periphery of its range for which all habitats in the Tongass are suboptimal may rank higher than a rare species endemic to the Tongass. The importance of populations within the Tongass to the species as a whole carries less weight than aspects like dispersal behavior. This approach may be short-sighted, because the likelihood that a species will become threatened or endangered depends on its rarity beyond the region, and with listing comes a much stronger management mandate. Many of the characteristics that others have associated with rarity and vulnerability to extinction (Rabinowitz, 1981; Reed, 1990) are included in the criteria, but they are not weighted heavily.

It is commendable to make the criteria for selecting sensitive species explicit as is done here, but one must avoid the trap of thinking that by doing so one achieves objectivity. In fact the entire process is highly subjective. There are few data to justify associating some species with old-growth but not others, or assigning values for each species for each criteria, or for assigning weights to the criteria. One might do just as well by picking species with small population sizes and vulnerable life histories that represent the major habitat and microhabitat types. It would be most useful to run a discriminant analysis to determine what actually separated those species selected as sensitive from others. To answer any criticisms about which species are selected, it is essential to be able to state which characteristics caused this set to be selected rather than candidates put forth by others. Some selections invite criticism, for example inclusion of the great blue heron but not the marbled murrelet. Given the likelihood that the murrelet will be listed as endangered or threatened and its documented ties to old-growth forest, its exclusion from both the sensitive species and management indicator species lists seems to me a mistake.

The process of generating HCAs, like the process of generating sensitive species, is an excellent one conceptually, but highly subjective in practice. The

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process reflects metapopulation thinking, and awareness of issues such as habitat fragmentation. Because of this I anticipate that the approach will hold up well to scrutiny in future years. The details of the process, on the other hand, almost certainly will not. The habitat quality requirements for HCAs, the number of individuals that must be contained in each one, and the minimum distances required between them are basically educated guesses. The process again is vulnerable to criticisms about details due to a lack of relevant data. Even the data that are available are not the relevant data, but instead provide some indirect means of estimating what is relevant. For example, dispersal distance distributions do not really tell us how far apart HCAs should be. Rates of exchange between HCAs various distances apart would be the relevant data, but such data do not exist, and there is no supporting evidence that rates of exchange can be accurately predicted from dispersal distance distributions.

It is of course virtually impossible to collect the relevant data in a reasonable time frame. The HCAs do not even exist currently. My recommendation is to use individual-based simulation modeling (DeAngelis and Gross, 1992) to evaluate the effectiveness of the conservation strategy. Such models can be used to assess population dynamics on alternative landscapes consisting of different numbers and arrangements of HCAs. Results would include estimates of things like how much exchange there would be between HCAs over different distances, and how much demes within HCAs of different sizes would fluctuate. More importantly, the models could be used in sensitivity analysis. Through sensitivity analysis, one could estimate how much more (or less) habitat would need to be protected under the most pessimistic (or optimistic) estimates of model parameters, compared to the parameter values used originally. One could determine, using the application presented in "*Strategy*", how close to desired populations levels actual populations would be given different amounts of error in the original parameter estimates. Recommendations based on minimizing chances of extinction, derived in this way, would be much easier to defend than recommendations based on educated guesses. Changes in amount of habitat protected could be expressed in terms of more or less risk of extinction. Managers could use these functions to optimize their decisions with respect to single or multiple factors, including wildlife conservation.

If this approach is used, improving the precision of the models and thereby reducing the range of appropriate conservation strategies would require obtaining the data needed to better estimate model parameters. In these models the parameters would be survival, reproductive and dispersal rates of individuals, rather than attributes of demes. The former data can be collected more easily and more quickly than the latter data. This is why I recommend individual-based modeling over other metapopulation models whose parameters are attributes of demes. Otherwise, these other models can fulfill the same functions described above for individual-based modeling, and they have the advantage of being analytical rather than pure simulations. Arguments can be

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made for either approach, and for many important species even the data needed to estimate individual-based model parameters will be difficult to obtain.

The results of the evaluation of the single application described are quite convincing: the existing forest management plan fails to achieve what according to the "*Strategy*" is required to maintain well distributed populations of vertebrates. A parallel analysis on a different, although somewhat overlapping set of species in the "Risk Assessment" document produces the same result. If one accepts that the objective to maintain populations in all the provinces is reasonable, and that the method for achieving this described in the "*Strategy*" is appropriate, then it is impossible to escape the conclusion that the existing plan is inadequate. One might argue that since habitat outside of HCAs, which certainly will harbor some individuals of the species analyzed, is not considered, the analyses overestimate the effects of timber cutting. However, the HCAs are designed only to house minimum populations. Maintaining populations above minimum levels depends on areas outside the HCAs. It would be appropriate to add individuals living outside of HCAs to total population estimates only if a new standard for population size above minimum is defined.

I will offer a few comments about the particulars of the analyses of individual sensitive species. Again, I am not convinced the great blue heron should be included in the analysis, given that the Tongass seems to represent a marginal area for this widespread species in the best of circumstances. There is only one study that offers any substantial evidence that this species is adversely affected by disturbance (Gibbs *et al.*, 1987), and in this study area in Maine there were relatively few alternative nesting sites for herons. Relocation of nests is unlikely to be as big a problem in the Tongass where there are so few herons and so many potential nesting sites. Efforts expended on providing for this species are probably better expended elsewhere. The goshawk, on the other hand, is an ideal choice as a sensitive species. Its populations are small, its area requirements large, and its links to old-growth fairly well documented. One study (Crocker-Bedford, 1987) offers convincing experimental evidence that logging of old-growth adversely affects the species. Although this study was conducted in another region, that correlations between timber cutting and population decline are widespread suggests that the experimental results can be extrapolated to the Tongass. I found opposing arguments about the need for a diversity of stand ages to be totally unconvincing. For goshawks the reduction in number of pairs per HCA from the originally stated standard of 20 is poorly justified. One could easily question whether the "*Strategy*" is sufficient in the case of this species, even accepting the details of the overall process.

The boreal owl presumably was included in the document because it is the highest ranking bird species among those not included as sensitive. However, the Tongass appears to be a peripheral area for this species, and thus there is little reason to consider its requirements in developing a management plan. Again, the marbled murrelet, as well as the Vaux's swift, are more reasonable candidates

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because of links to old-growth in both cases, and rarity in the case of the *murrelet*.

A good case can be made for including the wolf and brown bear based on population size, life history and rarity. For wolves, however, the evidence presented here and in the "HCM" document indicate no link to old-growth. Therefore other habitat types besides old-growth should be included in population projections. Evidence of adverse effects of road development is convincing for both wolves and bears. For both species the issue of hunting seems to be avoided. For bears especially, given the convincing arguments about their vulnerability to increased mortality, it is surprising that the effect of hunting is not evaluated. This obviously is a concession to factors other than biology and should be stated as such. Trapping of martens is a similar issue. It would be useful to quantify the incompatibility between timber cutting and hunting and trapping by producing a function that shows, given the population size goals, how much hunting will have to be reduced in order to allow additional timber cutting. One could also show how much more hunting could be allowed if timber cutting were reduced beyond the level allowed in the application presented.

The reasons for considering river otters and mountain goats as old-growth species are not clear from material included in "*Strategy*", although material in the "HCM" document provides some justification. This linkage is well established for flying squirrels. For this species there is an inconsistency between data on density and the area requirements specified.

There are problems with details common to development of HCA requirements for all species. A major one is that habitat use is equated to habitat value, a problem that also arises in "HCM". Here the problem takes the form of using density as an estimate of value. An appropriate definition of value would be based on fitness, that is, relationships of habitat to reproductive success and survival. Implicit in use of density data to estimate habitat value is the assumption that species are at carrying capacity. In some analyses, however, this assumption is violated by allowing for factors such as increased mortality correlated with road development. Fortunately the errors caused by this procedure are conservative, because HCAs will actually hold more individuals than projected if density data are from populations below carrying capacity. Other problems include a general lack, with some exceptions, of data justifying requirements for corridors or projected negative effects of loss of old-growth. Again, the approach is conservative in generally assuming the worst.

A second set of species to use in evaluating management is listed in "Risk Assessment". The process by which these species were selected is not described in the documents I reviewed, but it evidently allowed for selection of species other than those dependent on old-growth. The material presented indicates that there is a need to manage for six bird and one frog species because they are category

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2 or sensitive species. One of these (goshawk) was identified as a sensitive (in a different sense of the word) species in "*Strategy*", and another (goose) is included among the management indicator species. It is stated that there are guidelines for the remaining species (murrelet, duck, frog, osprey, swan). I suggest the impacts of the proposed management strategy on these species should be included in analyses presented in the planning documents.

It is not obvious, without viewing supporting documents, that the species selected as management indicators best represent the major habitats and microhabitats. These ideally should be species that are highly habitat-specific and have well-defined microhabitats. At least some should represent the rarest microhabitats, and all major habitats should be represented by at least one or two species. Selection of indicator species appears to be governed more by economic incentives than by the relevant biological criteria, at least in the case of mammals.

The discussion of the limitations of habitat capability models is excellent and appropriate. Of course these models are not used in "Risk Assessment". Instead risk is evaluated in terms of total loss of old-growth and effects on HCAs. These analyses provide relative rankings among provinces with respect to risks that are clear and consistent. What cannot be determined is how different degrees of risk translate into changes in numbers of particular species. The analysis is successful in indicating where adverse impacts are likely to occur under the existing forest plan, but not what those impacts are likely to be.

I find it interesting that risk is assessed through the conservation strategy rather than through the habitat capability models. I prefer this approach, and recommend further evaluation of effects of management on indicator species in terms of the conservation strategy, rather than proceeding with plans to assess risk through habitat capability models. Instead of evaluating effects on the HCAs, further efforts should evaluate effects on particular indicator species distributed among the HCAs, using (again) individual-based models.

Given all the limitations of habitat capability models articulated in "Risk Assessment", and others evident from evaluating the individual models, it is not clear that these models will be particularly useful. Time and money might better be spent on other approaches such as individual-based simulation modeling. Those involved in planning clearly state that these models are only useful in comparing the abundance of habitat of various qualities under different management alternatives. They are not useful in determining what levels of habitat, and thus which management alternatives, are sufficient to provide for viable populations. This can only be achieved if the models can accurately predict density, and for this purpose they are inadequate. The degree of inadequacy depends on the extent to which habitat use equates to habitat value. It is probably safe to assign values of 0 to habitats that are not used at all, but assignment of values beyond that level are highly arbitrary. The problem

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becomes larger as the amount of space used by individuals increases. For species whose entire range is contained in a single habitat patch, density measures might relate to carrying capacity in a fairly straightforward way, and thus could be used to estimate habitat value. Still, extrapolating across the forest requires assuming that all patches will be filled to capacity, and ignoring all the landscape-level concerns at the core of the approach described in "*Strategy*". For species in which individuals use multiple habitat patches, the relationships between use, habitat value and carrying capacity become even more complex and difficult to interpret. For these species one has no idea whether constraints that cause a species to make use of less preferred nest sites or habitat types will cause a large effect on fitness or a trivial one.

The analyses indicate the habitat capability models to be highly sensitive to parameter values, making results even more suspect. The use of these models is inconsistent with the approach outlined in "*Strategy*". Selecting and evaluating management indicator species is highly desirable, but evaluations need to be more consistent with those for sensitive species. A switch from habitat capability models to metapopulation or individual-based models would accomplish this. Another reason for switching approaches is that individual-based modeling and metapopulation modeling surely will become more sophisticated in future years, so that their usefulness in planning will increase. The limitations of habitat capability models, on the other had, are inherent to the process by which they were constructed, and therefore can never be reduced. They represent a dead end, the other approaches an open highway.

I provide detailed reviews of the models for the two woodpecker species and brown creepers in the next section. I will make only a few comments about the remaining models, most of which I did not review in detail. The model for wolves seemed to me odd in that it is based entirely on the prey base, and thus ignores the factors (e.g., human contact related to roads) indicated to be important in "*Strategy*". This may reflect the fact that the modeling approach assumes the species is at carrying capacity when in fact it probably is not. The brown bear model predicted densities quite well, but the deer model did not. Although the authors of the model seem content with a prediction that is only 75% of actual density, I find this to be too great a disparity to ignore.

Overall, then, I found the approach taken in "*Strategy*" to be an excellent one. Some elements of the proposed management are truly clever, such as using corridors between HCAs. The approach results in a highly integrated plan that accounts for all species, at least within old-growth, as opposed to the sort of inconsistent plan derived by merging a number of single-species management plans together that one often sees. It is the specifics of the proposed strategy that can be challenged. This problem is best addressed through sensitivity analysis using a modeling approach that is consistent conceptually with the management strategy. Individual-based models or other metapopulation models are well suited to this purpose. It is useful to evaluate the effectiveness of the

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management described in "*Strategy*" further using Management Indicator Species, but this evaluation needs to follow the same approach as other evaluations. This consideration calls the utility of habitat capability modeling into question. Finally, the plan must also justify, based on considerations other than biological ones, adopting the strategy selected rather than one more favorable to wildlife, for example a strategy based on uneven-aged timber management.

3. Species Review

Hairy Woodpecker

This species is probably a good choice for a management indicator species. There apparently are data from the region linking it to old-growth in the thesis by Harris referenced in the document. (This is a key reference that I was unable to find, but would very much like to examine. Its value in this review exemplifies the need for census data at the community level.) Throughout its range, it appears to be a specialist in the sense that it is associated with a specific, often ephemeral microhabitat or habitat patch type. Often its specialty is patches of recently dead trees, and usually it is uncommon. Where this is the case, if its needs are being met the habitat requirements of most other species probably are being met as well, since the microhabitat required by hairy woodpeckers is less abundant than most other microhabitats. This is a much better justification for using this species than concerns about it declining, since these concerns are based on suspect data. Evidence of decline consists only of Christmas count data, and only exists for urban areas (Morrison and Morrison, 1983). Away from urban areas these data indicate stable or even increasing populations.

The model equates tree value to tree size. There is no good evidence for this or any other woodpecker that reproductive success is higher in larger trees. There is evidence that excavation is easier in larger trees (Conner, 1979), but if this is the basis for preference, the effect of tree size on habitat value could be trivial. The usual problems with assigning values to habitat apply.

Red-breasted Sapsucker

Including this species among the management indicators is justified by its importance to the community as a primary cavity excavator. However, given the data indicating woodpecker populations to be limited during winter (Raphael and White, 1984), it is especially inappropriate to apply HCM modeling to breeding populations of this species. Because of this, it would be surprising if the model for this species worked well. The process of assigning habitat values is unusually suspect in this case because it deviates from what the density data indicate, resulting in higher values for medium and high volume stands.

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Brown Creeper

This species is an excellent choice as a representative of those dependent on old-growth. Census data consistently indicate an extremely strong link between this species (and other bark gleaners) and old-growth (Franzreb and Ohmart, 1978; Raphael and White, 1984; Airola and Barrett, 1985; Manuwal and Huff, 1987). That the species will be sensitive to logging might be inferred from its dependence on old-growth. The experimental study cited as evidence of an effect of logging (Franzreb and Ohmart, 1987) fails to demonstrate a treatment (logging) effect due to lack of replication and of appropriate repeated measures within plots. Since territories are small for this species, this model may well be among the most accurate in predicting density.

Summary

My assessments of all three models are similar. All three species are good choices as management indicators, although for different reasons. A single data set exists relating densities of all three to habitat type. Obviously this study should be repeated in other plots and other years to better quantify relationships between density and habitat. Simple models based on equating density with habitat value could be built using these data, but the usefulness of such models can be questioned. These models may come closer to projecting population potential than models for mammalian species in which individuals use multiple habitats, but they still have major inadequacies. Data relating fitness to habitat could improve such models, but such data are lacking for all three bird species.

4. Comprehensive Recommendations For The Future

My recommendations about future efforts are stated at appropriate points in the preceding sections. I will summarize them here. I am happy with the concepts and approaches contained in "*Strategy*" and "Risk Assessment", but not those in "HCM". I think the best course of action is to improve the precision of the process outlined in "*Strategy*". The process of selecting sensitive and management indicator species might be revisited, at least to make sure there are no important (i.e., rare, such as murrelet) species, habitats or microhabitats that are not represented between the two lists. A crucial need is to justify the details of the conservation strategy proposed through individual-based simulation or metapopulation modeling. This process will lead to a range of strategy options that represent different degrees of risk to animal populations. It is quite likely that this process will cause planners to select a strategy that differs somewhat in its details from the one currently proposed. Finally, the conceptual framework for thinking about habitat could be improved, by better defining habitat and

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microhabitat types, and be better defining habitat relationship of the animal species within the community.

Research needs reflect the approach recommended above. The modeling efforts described are a major need. From the field, studies of habitat relationships at the community level are needed. These studies should provide density estimates from different habitats and microhabitats, enabling managers to assign species to habitat groups. This information will enable managers to determine which species a given indicator species represents, and to make sure that all habitat groups are represented among the indicator species. Other field data requirements are dictated by the modeling efforts. If individual-based simulation modeling is used, it will be important to collect data on reproduction, survival and movement of sensitive and indicator species in order to improve the precision of the modeling, and thereby the details of the conservation plan. Those species whose biology impacts the strategy the most should receive the highest priority in such studies. If metapopulation models are used, it will be important to collect data on the behavior of demes, that is, population dynamics within HCAs and movement between HCAs, for sensitive and indicator species.

Monitoring must be structured to track trends over long periods of time. The initial need is to obtain baseline data, and subsequently there will be a need for data indicating populations trends. Ideally, one would like such data for all sensitive and indicator species, from a sample of HCAs of all sizes. This may not be practical, although it becomes more practical as the interval between sampling a given species increases. Monitoring needs are similar whether individual-based modeling or metapopulation modeling is used, except that the latter approach necessitates collecting data from a larger sample of HCAs. As a safeguard, it would be useful to repeat community-level sampling at intervals, to make sure that indicator species are representing their habitat groups well.

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Benkman. C.W. 1993. Logging. conifers. and the conservation of crossbills. Conservation Biology 7:473-479.

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1991. Designed, authored and implemented a counseling program guide for Job Corps programs. Adopted for implementation by several other DOL Job Corps Regions.

1991. Ph.D. dissertation research involved a statistical analysis of the styles of academic advising experienced by students in various demographic groups at two community colleges.

1985. Conducted a pilot study on the needs of non-traditional students and their families to discover implications for student retention, program development, structure, and students' needs for services.

1983. Designed and conducted a quantitative analysis of the characteristics of elementary and secondary education pre-service teaching majors.

1981. M.A. research project - qualitative, participant/observation study on parent education programs.

PRESENTATIONS:

1992. US Department of Labor, Job Corps Region X Residential Staff Training Module, North Bend, WA.

1986. Non-traditional students and their families: A pilot research study. NACADA Conference, October 1986, Seattle.

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1985. The orientation course: three successful approaches. Utah State Advisors' Conference, May, 1985, Park City.

1984. Expanding your horizons: math and science where you least expect it. Presentation and panel moderator. Utah Consortium of Women in Higher Education, Logan, UT.

PROFESSIONAL ASSOCIATIONS:

National Council on Family Relations
National Academic Advising Association
National Research Committee
National Task Force on Adult Students

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ERIC D. FORSMAN

SUPERVISORY RESEARCH WILDLIFE BIOLOGIST
Pacific Northwest Research Station
USDA Forest Service

EDUCATION:

Ph.D. 1980. Oregon State University. Wildlife Management.

M.S. 1975. Oregon State University. Wildlife Management.

B.S. 1972. Oregon State University. Wildlife Science.

PROFESSIONAL EXPERIENCE:

1991 - present. Supervisory Research Wildlife Biologist, U.S. Forest Service. Forestry Sciences Laboratory, Corvallis, OR.

1989 - 1991. Supervisory Research Wildlife Biologist, U.S. Forest Service, Forestry Sciences Laboratory, Olympia, WA.

1987 - 1989. Research Wildlife Biologist. U.S. Forest Service. Forestry Sciences Laboratory, Olympia, WA.

1983 - 1987. Wildlife Consultant. Nine research contracts on the spotted owl, one on the gray owl, for the following agencies: Oregon State Department of Fish and Wildlife, U.S. Forest Service, Pacific Northwest Region, U.S. Forest Service, Siuslaw National Forest, British Columbia Ministry of Environment, Bureau of Land Management.

1983. Research Assistant. Oregon Cooperative Wildlife Research Unit.

1982. Research Assistant. Oregon Cooperative Wildlife Research Unit, Pacific Northwest Forestry Research Laboratory and Oregon State University.

1980. Temporary Wildlife Biologist. Bureau of Land Management. 1980. Wildlife Consultant. U.S. Forest Service, Fremont National Forest.

1976. Wildlife Consultant. Oregon Department of Fish and Wildlife.

PROFESSIONAL ASSOCIATIONS:

The Wildlife Society
American Ornithologists Union
Cooper Ornithological Society
The Wilson Society
Pacific Northwest Bird & Mammal Society
American Society of Mammalogists
Oregon Field Ornithologists

AWARDS AND HONORS:

Outstanding Achievement Award for Contributions to Development of the Conservation Strategy for the Northern Spotted Owl. 1991. U.S. Forest Service, Bureau of Land Management, National Park Service, U.S. Fish and Wildlife Service.

Wildlife Society Group Achievement Award for 1991. As a member of the Interagency Spotted Owl Scientific Committee.

Service Award. 1990. As a member of the Interagency Spotted Owl Scientific Committee. U.S. Forest Service.

Certificate of Merit. 1990. Superior performance as a member of the Interagency Scientific Committee on the Northern Spotted Owl.

Wildlife Society Award for Best Monograph, 1984.

Oregon Chapter of the Wildlife Society award for best presentation by a student, 1980.

PUBLICATIONS:

Hamer, T.E.; Forsman, E.D.; Fuchs, A.D.; Walters, M.L. In press. First records of hybridization between barred and spotted owls. Auk.

Thomas, J.W.; Raphael, M.G.; Anthony, R.G.; Forsman, E.D.; Gunderson, A.G.; Holthausen, R.S.; Marcot, B.G.; Reeves, G.H.; Sedell, J.R.; Solia, D.M. 1993. Viability Assessments and Management Considerations for Species

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Associated with Late-successional and Old-growth Forests in the Pacific Northwest. USDA Forest Service, Portland, OR. 530 p.

Thomas, J.W., *et al.* including incumbent. 1993. Report of the Forest Ecosystem Management Assessment Team.

Bart, J.; Forsman, E.D. 1992. Dependence of northern spotted owls (*Strix occidentalis caurina*) on old-growth forests in the western USA. Biological Conservation 62:95-100.

Foster, C.C.; Forsman, E.D.; Meslow, E.C.; Miller, G.S.; Reid, J.A.; Wagner, F.F.; Carey, A.B.; Lint, J.B. 1992. Survival and reproduction of radio-marked adult spotted owls. J. Wildl. Manage. 56:91-95.

Everett, R.; Martin, S.; Bickford, M.; Schellhaas, R.; Forsman, E. 1991. Variability and dynamics of spotted owl nesting habitat in eastern Washington. In: Proceedings of the National Silviculture Workshop, May 6-9, 1991, Cedar City, UT. Pp. 35-39.

Dunbar, D.L.; Booth, B.P.; Forsman, E.D.; Hetherington, A.E.; Wilson, D. 1991. Status of the spotted owl (*Strix occidentalis*), and barred owl (*Strix varia*), in southwestern British Columbia. Canadian Field Naturalist 105:464-468.

Forsman, E.D.; Sovern, S.; Taylor, M. 1990. Home range and habitat of northern spotted owls on the east slope of the Cascade Mountains, Washington. Northwest Environmental Journal 6(2):430-431.

Thomas, J.W.; Forsman, E.D.; Lint, J.B.; Meslow, E.C.; Noon, B.R.; Verner, J. 1990. A conservation strategy for the northern spotted owl. U.S. Forest Service, Bureau of Land Management, U.S. Fish and Wildlife Service, and U.S. National Park Service. 427 p.

Forsman, E.D. 1988. A survey of spotted owls in young forests in northwestern Oregon. Murrelet 69(3):65-68.

Forsman, E.D.; Bull, E. 1988. Status of large owls in the western United States. In: Proceedings of the symposium on status of raptors in the western United States. Boise, ID. The National Wildlife Federation. Pp. 118-123.

Forsman, E.D. 1987. The spotted owl: literature review. In: Final supplement to the environmental impact statement for an amendment to the Pacific Northwest Regional Guide. USDA Forest Service, Portland, OR.

Anthony, R.G.; Forsman, E.D.; Green, G.A.; Witmer, G.; Nelson, S.K. 1987. Small mammal populations in riparian zones of different-aged coniferous forests. Murrelet 68:94-102.

Bryan, T.; Forsman, E.D. 1987. Distribution, abundance, and habitat of great gray owls in southcentral Oregon. Murrelet 68:45-49.

Forsman, E.D.; Bruce, C.R.; Walter, M.A.; Meslow, E.C. 1987. A current assessment of the spotted owl population in Oregon. Murrelet 68:51-54.

Forsman, E.D.; Meslow, E.C. 1986. The spotted owl. In: Audubon Wildlife Report, 1986. National Audubon Society, New York, NY. Pp.743-761.

Forsman, E.D.; Horn, K.M.; Mires, G.W. 1985. Northern spotted owls. In: Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington. Part 1: Narratives. USDA Forest Service, Pacific Northwest Region, Portland, OR. Pp. 259-267, Chapter 12.

Forsman, E.D.; Meslow, E.C.; Wight, H.M. 1984. Distribution and Biology of the Spotted Owl in Oregon. Wildlife Monograph No. 87. 64 p.

Forsman, E.D. 1983. Spotted owl. (*Strix occidentalis*). In: Arbruster, J.S., ed. Impacts of Coal Surface Mining on 25 Migratory Bird Species of High Federal Interest. U.S. Fish and Wildlife Service, Washington, D.C. Pp. 243-255.

Forsman, E.D.; Horn, K.M.; Neitro, W.A. 1982. Spotted owl research and management in the Pacific Northwest. In: Transactions of the 47th North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington, D.C. Pp. 323-331.

Forsman, E.D. 1991. Molt of the spotted owl. Auk 98:735-742.

Forsman, E.D. 1980. Habitat utilization by spotted owls in the west-central Cascades of Oregon. Ph.D. Thesis. Oregon State University, Corvallis. 95 p.

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Forsman, E.D.; Wight, H.M. 1979. Allopreening in owls: what are its functions? Auk 96:525-531.

Forsman, E.D.; Meslow, E.C.; Strub, M.J. 1977. Spotted owl abundance in young versus old-growth forests. Oregon Wildlife Society Bulletin 5(2):43-47.

Taylor, Jr., A.L.; Forsman, E.D. 1976. Recent range extensions of the barred owl in western North America, including the first records for Oregon. Condor 78(4):560-561.

Forsman, E.D. 1976. A preliminary investigation of the spotted owl in Oregon. M.S. Thesis. Oregon State University, Corvallis, OR. 127 p.

Reynolds, R.T.; Forsman, E. 1971. A recent occurrence of a colony of white-throated swifts in Oregon. Murrelet 52(4):13-14.

Forsman, E.; Maser, C. 1970. Saw-whet owl preys on red tree mice. Murrelet 51(1):10.

10_012933

ANDREW JAMES HANSEN

ASSISTANT PROFESSOR
Montana State University

EDUCATION:

Ph.D. 1984. University of Tennessee/Oak Ridge National Lab. Ecology.

B.S. 1978. Western Washington University. Ecology. University of Colorado. Biology.

PROFESSIONAL EXPERIENCE:

1993-present. Assistant Professor, Montana State University.

1988-1993. Assistant Professor, Oregon State University.

1987. A. W. Mellon Foundation Research Fellow, Scientific Committee on Problems in the Environment, Montpelier, France.

1986-1987. Assistant Professor, Humboldt State University.

1986. Visiting Professor, University of Virginia.

1984-1986. Post Doctoral Research Fellow, University of the Witwatersrand, Johannesburg, South Africa.

PROFESSIONAL ASSOCIATIONS:

American Association for the Advancement of Science
Society for Conservation Biology
Ecological Society of America
International Association of Landscape Ecologists
American Institute of Biological Science

PUBLICATION SUMMARY:

Referred Journal Articles:	10
Book Chapters:	6
Non-referred Journal Articles:	6
Papers in Review	2
Edited Books	2

SELECTED PUBLICATIONS:

Hansen, A. J.; Garman, S.; Weigand, J.; Urban, D.; McComb, W.; Raphael, M. In prep. Ecological and economic effects of alternative silvicultural regimens in the Pacific Northwest. Ecological Applications.

Hansen, A. J.; Spencer, R.; Moldenke, A.; McKee, A. In Review. Ecological processes linking forest structure and avian diversity in western Oregon: A test of hypotheses. In: Boyle, T. Biodiversity, Temperate Ecosystems, and Global Change. Springer-Verlag, New York.

Hansen, A. J.; Hounihan, P. In Press. A Test of ecological forestry: Canopy retention and avian diversity in the Oregon Cascades. In: Szaro, R., ed. Biodiversity in Managed Landscapes: Theory and Practice. Oxford University Press, London.

Hansen, A. J.; Garman, S. L.; Marks, B.; Urban, D. L. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. Ecological Applications 3:481-496.

Hansen, A. J.; Urban, D. L. 1992. Avian response to landscape pattern: The role of species life histories. Landscape Ecology 7:163-180.

Hansen, A. J.; diCastri, F., eds. 1992. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag Ecological Studies Series, New York. 432 p.

Hansen, A. J.; Urban, D.; Marks, B. 1992. Avian community dynamics: The interplay of landscape trajectories and species life histories. In: Hansen, A. J.; deCastri, F., eds. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag Ecological Studies Series, New York. Pp. 170-195.

Hansen, A. J.; Risser, P.; diCastri, F. 1992. Epilogue: Biodiversity and ecological flows across ecotones. In: Hansen, A. J.; diCastri, F., eds. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag Ecological Studies Series, New York. Pp. 423-433.

Hansen, A. J.; Spies, T.; Swanson, F.; Ohmann, J. 1991. Conserving biodiversity in managed forests: Lessons from natural forests: Implications for conserving biodiversity in managed forests. BioScience 41(3):382-392.

diCastri, F.; Hansen, A. J.; Debussche, M., eds. 1990. Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers. Dordrecht, The Netherlands.

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OLIVER A. HOUCK

PROFESSOR
Tulane Law School

EDUCATION:

Georgetown Law Center, Evening Division, 1963-67, J.D. Cum Laude

American Jurisprudence Prizes: Agency, Contracts, International Law

Harvard University, 1956-60
B.A., English, Cum Laude
Dean's List 1958, 1959, 1960
Harvard Scholarship 1959, 1960

PROFESSIONAL EXPERIENCE:

1981 - present, Professor of Law, Tulane Law School, New Orleans, La. 1986 - present (Associate Professor, 1982 - 1986; Visiting Professor, 1981 - 1982); direction of environmental law program.

1971 - 1981, Counsel (1971-73), General Counsel (1973-79) and Vice President for Conservation and Education (1979-81), National Wildlife Federation, Washington, D.C.: direction of legal, legislative, research and educational programs.

1968 - 1971, Assistant United States Attorney, Office of the U.S. Attorney for the District of Columbia, Washington, D.C.: criminal trial, grand jury, major crimes.

1966 - 1968, Law Clerk to Judge Timothy Murphy, Superior Court of the District of Columbia.

1964 - 1966, Military Capabilities Analyst, Defense Intelligence Agency, U.S. Department of Defense.

1961 - 1964, United States Army, foreign and domestic intelligence collection.

ADMITTED TO PRACTICE:

District of Columbia; United States Supreme Court

TEACHING EXPERIENCE:

Tulane Law School, 1981-present: Environmental Law, Natural Resources Law, Criminal Law, Criminal Procedure; seminars in Organized/White Collar Crime and in Wildlife, Coastal Zone, Toxic and Hazardous Wastes, Water Resources and International Environmental Law.

Adjunct Professor at Georgetown Law School (1981), George Washington Law School (1978- 80), Vermont Law School, (summer 1979-82), American University Law School (1979). Evening instructor in English writing, The Heights, Washington, D.C. (1968-69).

AWARDS:

Felix Frankfurter Distinguished Teaching Award, Tulane Law School, 1987.

New Orleanian of the Year, Gambit Magazine, 1986.

Faculty Award, Black Law Student Association, Tulane, Law School, 1986.

Conservationist of the Year, Louisiana, 1985.

C.J. Morrow Research Fellow, Tulane Law School, 1985-86.

Governor's Conservation Award, Louisiana, 1982.

PROFESSIONAL ASSOCIATIONS:

Board of Directors, Environmental Law Institute, Washington, D.C.
Board of Directors, Defenders of Wildlife, Washington, D.C.
Litigation Committee, Environmental Defense Fund, New York City.
Committee on the Role of Technology in Marine Habitat Protection, National Research Council, National Academy of Science.
Committee on Scientific Issues in the Endangered Species Act, National Research Council, National Academy of Science.
Area Council, American Lung Association of Louisiana.
Tulane University Environmental Project (chair)

Coalition to Restore Coastal Louisiana (co- founder)
Tulane Public Interest Law Foundation (co- founder)
Tulane Environmental Law Journal (co-founder and faculty advisor)
Tulane Environmental Law Society (co-founder)
Tulane Environmental Law Clinic (founder and Legal Review Committee member)

MAJOR LAW PUBLICATIONS:

"The Secret Opinions of the United States Supreme Court on Leading Cases in Environmental Law, Never Before Published!:, Colorado Law Review (accepted for publication, Summer, 1994).

"Of Bats, Birds and BAT: The Convergent Evolution of Environmental Law," Mississippi Law Journal (accepted for publication, Spring, 1994.

"The Endangered Species Act and its Implementation by the U.S. Departments of Interior and Commerce," Colorado Law Review, 1993.

"The Regulation of Toxic Discharges under the Clean Water Act," Environmental Law Reporter, September, 1991.

"Hard Choices: The Analysis of Alternatives Under Section 404 of the Clean Water Act and Related Environmental Laws," Colorado Law Review, July, 1989.

"Ending the War: Towards a Strategy to Save America's Coastal one," Maryland Law Review, Winter, 1988.

"President X and the New (Approved) Decisionmaking," American University Law Review, April, 1987.

"This Side of Heresy: Conditioning Louisiana's Ten Year Industrial Tax Exemption," Tulane Law Review, December, 1986.

"Rising Water: The National Flood Insurance Program and the State of Louisiana," Tulane Law Review, October, 1985.

"With Charity for All: The Qualification of Business- sponsored Public Interest Law Firms as Charities under the Internal Revenue Code," Yale Law Journal, July, 1984.

"Land Loss in Coastal Louisiana: Causes, Consequences and Remedies," Tulane Law Review, October, 1983.

"The Institutionalization of Caution under Section 7 of the Endangered Species Act: What Do You Do When You Don't Know?" Environmental Law Reporter, April, 1982.

"Judicial Review under the Fish and Wildlife Coordination Act: A Plaintiff's Guide to Litigation," Environmental Law Reporter, August, 1981.

OTHER LAW PUBLICATIONS:

Book Review, "Going Too Far: A Review of "Breaking the Vicious Circle, Toward Effective Risk Regulation," Environmental Law Reporter, February, 1994.

"Environmental Law in the Fifth Circuit, 1991-2," Loyola Law Review, August, 1993 (co-authored).

"Environmental Law in the Fifth Circuit, 1990-91," Loyola Law Review, December, 1992 (co-authored).

"An Open Letter to EPA Administrator William K. Reilly," National Wetlands Newsletter, July/August, 1991.

"More Net Loss of Wetlands": The Army-EPA Agreement on Mitigation," Environmental Law Reporter, June, 1990.

Book Review, "The Second Battle of New Orleans: A History of the Vieux Carre River Front Expressway Controversy," Tulane Law Review, December, 1982.

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ROBERT L. JARVIS

PROFESSOR
Oregon State University

EDUCATION:

B.S. 1963. Humboldt State College. Wildlife.

M.S. 1965. Humboldt State College. Wildlife.

Ph.D. 1969. Southern Illinois University. Zoology.

PROFESSIONAL EXPERIENCE:

1986 - present. Professor, Department of Fisheries and Wildlife, Oregon State University.

1978 - 1986. Associate Professor, Department of Fisheries and Wildlife, Oregon State University.

1971 - 1978. Assistant Professor, Department of Fisheries and Wildlife, Oregon State University.

1969 - 1971. Assistant Professor, School of Forestry and Wildlife Management, Louisiana State University.

1967 - 1969. Graduate Fellow, Southern Illinois University.

1965 - 1967. Teaching Assistant, Southern Illinois University.

1963 - 1964. Wildlife Biologist (Research) Division of Refuges, U.S. Fish and Wildlife Service.

1961 -1962. (Summers) Student Trainee, Division of Refuges, U.S. Fish and Wildlife Service.

PROFESSIONAL ASSOCIATIONS:

American Ornithologists Union
The Wildlife Society
Sigma Xi
Cooper Ornithological Society
Wilson Ornithological Society
Association of Field Ornithologists

PUBLICATIONS:

Mauser, D.M.; Jarvis, R.L.; Gilmer, D.S. 1994. Movements and habitat use of mallard broods in northeastern California. J. Wildl. Manage. 58(1):88-94.

Mauser, D.M.; Jarvis, R.L.; Gilmer, D.S. 1994. Survival of radio-marked mallard ducklings in northeastern California. J. Wildl. Manage. 58(1):82-87.

Bromley, R.G.; Jarvis, R.L. 1993. Energetics of migration and reproduction of Dusky Canada geese. Condor 95:193-210.

Jarvis, R.L.; Bromley, R.G. 1992. Managing racially mixed flocks of Canada Geese. Proceed. Internat. Canada Goose Symp. (In press).

Jarvis, R.L.; Passmore, M.F. 1992. Ecology of band-tailed pigeons in Oregon. U.S. Fish Wildl. Serv., Fish Wildl. Biol. Report 6. 38 p.

Euliss, N.H., Jr.; Jarvis, R.L.; Gilmer, D.S. 1991. Standing crops and ecology of aquatic invertebrates in agriculture drainwater ponds in California. Wetlands 11(3):179-190.

Euliss, N.H., Jr.; Jarvis, R.L.; Gilmer, D.S. 1991. Feeding ecology of waterfowl on evaporation ponds in California. Condor 93(3):583-590.

Mauser, D.M.; Jarvis, R.L. 1991. Attaching radio transmitters to 1-day old mallard ducklings. J. Wildl. Manage. 55(3):488-491.

Stern, M.A.; Jarvis, R.L. 1991. Sexual dimorphism and assortative mating in Black Terns. Wilson Bull. 103(2):266-271.

Euliss, N.H.; Jarvis, R.L.; Gilmer, D.S. 1989. Carbonate deposition on tail feathers of ruddy ducks using evaporation ponds. Condor 91(4):803-806.

Jarvis, R.L.; Cornely, J.E. 1988. Recent changes in wintering populations of Canada geese in western Oregon/southwestern Washington. In: Weller, M.W., ed. Waterfowl in Winter. U. Minn. Press, Minneapolis.

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Havel, L.H.; Jarvis, R.L. 1988. Formation of feeding flocks during winter by dusky and Taverner's Canada geese in Oregon. In: Weller, M.W., ed. Waterfowl in Winter. U. Minn. Press, Minneapolis.

Jarvis, R.L.; Noyes, J.H. 1986. Foods of canvasbacks and redheads in Nevada: Paired males and ducklings. J. Wildl. Manage. 50(2):199-203.

Cornely, J.E.; Campbell, B.H.; Jarvis, R.L. 1985. Productivity, mortality and population status of dusky Canada geese. N. Am. Wildl. and Natur. Resourc. Conf. 50:540-548.

Noyes, J.H.; Jarvis, R.L. 1985. Diet and nutrition of breeding female redhead and canvasback ducks in Nevada. J. Wildl. Manage. 49:203-211.

Dzinbal, K.A.; Jarvis, R.L. 1984. Coastal feeding ecology of harlequin ducks in Prince William Sound, Alaska, during summer. In: Nettleship, D.N.; Sanger, G.A.; Springer, P.F., eds. Marine birds: their feeding ecology and commerical fisheries relationships. Proceedings Pacific Seabird Group Symposium. Spec. Publ. Canad. Wildl. Serv. 6-10.

Talent, L.G.; Jarvis, R.L.; Krapu, G.L. 1983. Survival of mallard broods in south central North Dakota. Condor 85:74-78.

Talent, L.G.; Krapu, G.L.; Jarvis, R.L. 1982. Habitat use of mallard broods in south central North Dakota. J. Wildl. Manage. 46(3): 629-635.

Jarvis, R.L. 1982. Soybean impaction in waterfowl. In: Hoff, G.L.; Davis, J., eds. Non-infectious Diseases of Wildlife. Iowa State Univ. Press, Ames, IA.

Talent, L.G., Krapu, G.L.; Jarvis, R.L. 1981. Effects of redhead nest parasitism on mallards. Wilson Bull. 93(4):562-563.

Jarvis, R.L. 1980. Nesting ecology of ducks at Malheur National Wildlife Refuge. Final Contract Report, U.S. Fish and Wildlife Service.

Jarvis, R.L.; Bartonek, J.C., eds. 1979. Management and biology of Pacific Flyway Geese. OSU Book Stores, Inc., Corvallis, OR. 346 p.

Simpson, S.G.; Jarvis, R.L. 1979. Comparative ecology of several sub-species of Canada geese during winter in Western Oregon. In: Jarvis, R.L.; Bartonek, J.C., eds. Management and Biology of Pacific Flyway Geese. OSU Book Stores, Inc., Corvallis, OR. 223-241.

Passmore, M.R.; Jarvis, R.L. 1979. Reliability of determining sex of band-tailed pigeons by plumage characters. Wildl. Soc. Bull. 7(2):124-125.

Jarvis, R.L.; Simpson, G.S. 1978. Habitat, survival productivity and abundance of pheasants in Western Oregon, 1947-75. J. Wildl. Manage. 42(4):866-874.

Jarvis, R.L.; Furniss, S.B. 1978. Distribution and survival of mallards banded at Malheur National Wildlife Refuge. Northwest Sci. 52(2, Part 2):292-302.

Clark, S.; Jarvis, R.L. 1978. Effects of winter grazing by geese on yield of ryegrass seed. Wildl. Soc. Bull. 6(2):84-87.

Eltzroth, M.S.; Jarvis, R.L. 1976. Sight record of a Blue Grosbeak in Oregon. Murrelet 57:44-46.

Jarvis, R.L. 1976. Soybean impaction in Canada geese. Wildl. Soc. Bull. 4(4):175-179.

Jarvis, R.L.; Engbring, J. 1976. Survival and reproduction of wild and game-farm pheasants in Western Oregon. Northwest Sci. 50(4):222-230.

Jarvis, R.L.; Harris, S.W. 1971. Land-use patterns and duck production at Malheur National Wildlife Refuge. J. Wildl. Manage. 35(4):767-773.

Jarvis, R.L. 1969. Ecological and physiological aspects of soybean impaction in Canada geese. Ph.D. Dissertation, Southern Illinois University, Carbondale. 106 p.

Jarvis, R.L.; Harris, S.W. 1967. Canada goose nest success and habitat use at Malheur Refuge. Murrelet 48(3):46-51.

Jarvis, R.L. 1966. Occurence of European or Aleutian green-winged teal in Western North America, with a recent record. Murrelet 47(1):15-18.

Jarvis, R.L. 1965. Relationships between land-use patterns and waterfowl productions at Malheur National Wildlife Refuge, 1964. M.S. thesis, Humboldt State College, Arcata, CA. 95 p.

10_012938

A. ROSS KIESTER

GLOBAL BIOLOGICAL DIVERSITY TEAM LEADER
Pacific Northwest Research Station
USDA Forest Service

EDUCATION:

Ph.D. 1975, Harvard University. Biology.

1967 - 1968. Rockefeller University. Studied biochemistry, population genetics, animal behavior, mathematics.

A.B. 1967, with honors. University of California, Berkeley. Zoology.

PROFESSIONAL EXPERIENCE:

1989 - present. Supervisory Mathematical Statistician. USDA Forest Service - Pacific Northwest Forest Experiment Station.

1990 - present. Professor (Research), Courtesy. Department of Zoology, Oregon State University.

1986 - 1989. Mathematical Statistician. USDA Forest Service - Pacific Northwest Forest Experiment Station.

1985 - 1986. Mathematical Statistician. USDA Forest Service, Southern Forest Experiment Station.

1982 - present. Research Associate. Smithsonian Tropical Research Institute.

1984 - 1985. Associate Professor, Department of Biology and Center for Latin American Studies, Tulane University.

1982 - 1984. Assistant Professor, Department of Biology and Center for Latin American Studies, Tulane University.

1975 - 1982. Assistant Professor, Department of Biology, University of Chicago. Committees on Evolutionary Biology, Conceptual Foundations of Science, Latin American Studies. 1972 - 1975. Junior Fellow, Society of Fellows, Harvard University.

PROFESSIONAL ASSOCIATIONS:

American Statistical Association
The Biometric Society
American Society of Ichthyologists and Herpetologists
Society for the Study of Amphibians and Reptiles
Herpetologists League
C (Programming Language) Users Group
Society for Conservation Biology
International Society of Tropical Foresters

PUBLICATIONS:

Bormann, B.T.; Brookes, M.H.; Ford, E.D.; Kiester, A.R.; Oliver, C.D.; Weigand, J.F. 1994. Eastside Forest Ecosystem Health Assessment, Vol. V.: A Broad, Strategic Framework for Sustainable-Ecosystem Management. General Technical Report PNW-GTR-331. 61p.

Gordon, J.C.; Bormann, B.T.; Kiester, A.R. 1992. The physiology and genetics of ecosystems: A new target or "forestry contemplates an entangled bank." In: Colombo, S.J.; Hogan, G.; Wearn, V. Proceedings of the *twelfth North* American Forest Biology Workshop. Aug. 17-20, 1992. Pp. 1-14.

Cowling, E.B.; Shrtner, D.S.; Barnard, J.E.; Lucier, A.A.; Johnson, A.H.; Kiester, A.R. 1990. Airborne chemicals and forest health in the United States. In: Congress Report, Vol. B., UIFRO Montreal, Science in Forestry: IUFRO's Second Century. The Canadian IUFRO World Congress Organizing Committee, Montreal. Pp. 25-36.

Kiester, A.R.; *et al.* 1990. NAPAP Report 17: Development and use of tree and forest response models. In: Acidic Deposition: State of Science and Technology. National Acid Precipitation Assessment Program, Government Printing Office, Washington, D.C. 250 p.

Bassow, S.L.; Ford, E.D.; Kiester, A.R. 1990 A critique of carbon-based tree growth models. In: Dixon, R.; *et al.*, eds. Forest Growth: Process Modeling of Responses to Environmental Stress. Timber Press: Portland, OR. Pp. 50-57.

Kiester, A.R.; Ford, E.D. 1990. Modeling the effects of pollutants on the processes of tree growth. In: Dixon, R.; *et al.*, eds. Forest Growth: Process Modeling of Responses to Environmental Stress. Timber Press: Portland, OR. Pp. 324-337.

10_012939

Kiester, A.R. 1990. Process modeling of tree and forest growth: Current perspectives and future needs. In: Dixon, R.; *et al.*, eds. Forest Growth: Process Modeling of Responses to Environmental Stress. Timber Press: Portland, OR. Pp. 416-422.

Kiester, A.R.; Burke, L.M. 1989. Biological Diversity. In: Smith, J.; Tirpack, D., eds. The Potential Effects of Global Climate Change on the United States. US EPA:EPA-230-05-89-050.

Schroeder, P.; Kiester, A.R. 1989. National research on forest decline and air pollution: The Forest Response Program. Journal of Forestry 87:27-32.

Kiester, A.R. 1988. The roles of models in the Forest Response Program. In: Ek, A.R.; Shifley, S.R.; Burke, T.E., eds. Proceedings of the IUFRO Conference on Forest Growth Modeling and Prediction. Minneapolis MN. USDA FS NCFES G.T.R. NC-120.

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Kiester, A.R. 1975. Notes on the natural history of *Diploglossus millepunctatus*. Smithsonian Contrib. Zool. No. 176:39-43.

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University of Oregon

EDUCATION:

Ph.D. 1976. Harvard University. Biology.

Organization for Tropical Studies, San Jose, Costa Rica, Field Ecology, summer, 1973.

Graduate study in Theoretical Biology. 1972-73.

B.S. 1972. University of California, Irvine. Biology.

PROFESSIONAL EXPERIENCE:

1990 - present. Professor, Department of Biology, University of Oregon.

1989 - 1990. Louis Block Professor, Department of Ecology and Evolution, The University of Chicago.

1988 - 1989. Associate Professor, Department of Ecology and Evolution, The University of Chicago.

1982 - 1988. Associate Professor, Department of Biology, The University of Chicago.

1976 - 1978. Postdoctoral Fellow, Laboratory of Genetics, University of Wisconsin.

AWARDS AND HONORS:

Luigi Provasoli Award (with A.M. Wood and G.A Fryxell) for Outstanding Paper in the Journal of Phycology. 1986-87.

Natural Sciences and Engineering Research Council of Canada, Internation Scientific Exchange Award to spend summer 1988 in Dept. of Oceanography, Dalhousie, Univ., Halifax, Nova Scotia.

Vice President of the Society for the Study of Evolution, 1990.

First annual Sewall Wright Award, American Society of Naturalists, 1992.

SERVICE:

Reviewer of papers for: American Naturalist, Conservation Biology, Ecology, Evolution, Genetical Research, Genetics, Nature, Science, Theoretical Population Biology, and other journals.

Reviewer of grants for NSF, NIH, NSERC (Canada), NERC (Britain).

Occasional member of special site reviews by NIH Genetics Study Section.

Member of NSF panel on Conservation and Restoration Biology, Jan. 1992.

Member of National Audubon Panel on Restoration of the Everglades, 1991-1992.

PUBLICATIONS:

Lande, R.; Engen, S.; Saether, B.E. (submitted). Optimal harvesting of fluctuating populations with a risk of extinction.

Gimelfarb, A.; Lande, R. 1994a. Simulation of marker assisted selection in hybrid populations. Genetical Research. (In press).

Lande, R.; Schemske, D.W.; Schultz, S.T. 1994b. High inbreeding depression, selective interference among loci, and the threshold selfing rate for purging recessive lethal mutations. Evolution. (In press).

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EDUCATION:

Ph.D. 1957. University of Illinois.

M.S. 1954. University of Illinois.

B.S. 1953. Cornell University.

PROFESSIONAL EXPERIENCE:

1989 - present. Professor of Integrative Biology and Curator of Mammals, University of California, Berkeley.

1969 - 1989. Professor of Zoology and Curator of Mammals, University of California, Berkeley.

1966 - 1967; 1981 - 1983. Vice Chairman, Department of Zoology, University of California, Berkeley.

1974 - 1975. Acting Director, Museum of Vertebrate Zoology, University of California, Berkeley.

1968 - 1981. Associate Director, Museum of Vertebrate Zoology, University of California, Berkeley.

1965 - 1969. Associate Professor of Zoology and Associate Curator of Mammals, Museum of Vertebrate Zoology, University of California, Berkeley.

1959 - 1965. Assistant Professor of Zoology and Assistant Curator of Mammals, Museum of Vertebrate Zoology, University of California, Berkeley.

1957 - 1959. Instructor in Zoology and Assistant Curator of Mammals, Museum of Vertebrate Zoology, University of California, Berkeley.

1953 - 1956. Teaching Assistant, Department of Zoology, University of Illinois.

1953 - 1955 (Summers) Member, University of Illinois Museum of Natural History Expeditions to Arizona.

Summer 1952. Biologist-in-Charge, Labrador Oceanographic Expedition, Office of Naval Research.

Summer 1958. Wildlife Management Research Assistant, Utah State Agricultural College.

PROFESSIONAL ASSOCIATIONS:

American Society of Mammalogists
Ecological Society of America
British Ecological Society
Japanese Society of Population Ecology
Australian Mammal Society
Society for the Study of Evolution
American Society of Zoologists
American Ornithologists' Union
California Academy of Science
American Society of Naturalists
American Institute of Biological Sciences
American Association for the Advancement of Science
Sigma Xi
Phi Sigma
The (British) Mammal Society
Biological Society of Washington
Cooper Ornithological Society
International Association for Ecology Biosystematists
Society for Marine Mammalogy
Society for Conservation Biology
American Association for Zoological Nomenclature
Society for the Study of Mammalian Evolution

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PUBLICATIONS:

Lidicker, W.Z., Jr. In press. A spatially explicit approach to vole population processes. Polish Ecol. Studies.

Lidicker, W.Z., Jr.; Lidicker, L.N. In press. Mammals of the Marin Islands. In: Spight, R., ed. The Marin Islands National Wildlife Refuge.

Lidicker, W.Z., Jr. In press. *Zapus trinotatus orarius*. Rodent specialist Group (SSC). Action plans for North American rodents of conservation concern.

Lidicker, W.Z., Jr. 1994. Population Ecology. In: Birney, E.C.; Choate, J.R., eds. 75 Years of Mammalogy 1919 - 1994. Amer. Soc. Mamm. Spec. Publ. No. 11.

Lidicker, W.Z., Jr. 1993. Review: Murray, J.A. The great bear: Contemporary writings on the grizzly. Quart. Rev. Biol. 68:287.

Lidicker, W.Z., Jr.; Wolff, J.O.; Lidicker, L.N.; Smith, M.H. 1992. Utilization of a habitat mosaic by cotton rats during a population decline. Landscape Ecology 6:259-268.

Stenseth, N.C.; Lidicker, W.Z., Jr. 1992. The use of radioisotopes in the study of dispersal - with a case study. In: Stenseth, N.C.; Lidicker, W.Z., Jr., eds. Animal Dispersal: Small Mammals as a Model. Chapman and Hall Publ. London. Pp. 333-352.

Stenseth, N.C.; Lidicker, W.Z., Jr. 1992. Where do we stand methodologically about experimental design and methods of analysis in the study of dispersal? In: Stenseth, N.C.; Lidicker, W.Z., Jr., eds. Animal Dispersal: Small Mammals as a Model. Chapman and Hall Publ. London. Pp. 295-318.

Stenseth, N.C.; Lidicker, W.Z., Jr. 1992. Presaturation and saturation dispersal fifteen years later: Some theoretical considerations. In: Stenseth, N.C.; Lidicker, W.Z., Jr., eds. Animal Dispersal: Small Mammals as a Model. Chapman and Hall Publ. London. Pp. 201-223.

Lidicker, W.Z., Jr.; Stenseth, N.C. 1992. To disperse or not to disperse: who dies it and why? In: Stenseth, N.C.; Lidicker, W.Z. Jr., eds. Animal Dispersal: Small Mammals as a Model. Chapman and Hall Publ. London. Pp. 21-36.

Stenseth, N.C.; Lidicker, W.Z., Jr. 1992. The study of dispersal: a conceptual guide. In: Stenseth, N.C.; Lidicker, W.Z., Jr., eds. Animal Dispersal: Small Mammals as a Model. Chapman and Hall Publ. London. Pp. 5-20.

Stenseth, N.C.; Lidicker, W.Z., Jr., eds. 1992. Animal Dispersal: Small mammals as a Model. Chapman and Hall Publ. London (including Preface, Editors' Comments for 6 Parts of book, Epilogue). 365 p.

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EDUCATION:

Ph.D. 1984. Oregon State University. Wildlife Science.

M.S. 1978. Humboldt State University. Natural Resources Science, Wildlife Emphasis.

B.S. 1977. Humboldt State University. Natural Resources Planning and Interpretation.

A.A. 1975. College of the Redwoods. Biology.

PROFESSIONAL EXPERIENCE:

1990 - Present. Wildlife Ecologist and Spotted Owl Technical Coordinator. USDA Forest Service, Pacific Northwest Research Station. Leads technical aspects of ecological applications projects of the Ecological Framework for Management Research, Development, and Application Program. Evaluates research and monitoring priorities, devises and recommends new approaches. Develops old-growth forest reserve design. Develops and helps apply new approaches to managing for biological diversity and old-growth forest ecosystems on public lands. Develops and implements methods for analyzing and managing for wildlife population viability.

Staff Scientist Leader on President's Columbia River Basin Science Integration Team, President's Forest Ecosystem Management Working Group, Scientific Analysis Team, U.S. Congress' Scientific Panel on Late-Successional and Old-Growth Forest Ecosystems, Interagency Scientific Committee for the Northern Spotted Owl, Forest Service Spotted Owl EIS's. Advised population viability analysis and management under the Spotted Owl Recovery Team, California Spotted Owl Scientific Team, Sierra Nevada Ecosystem EIS team, Interagency Northern Spotted Owl Conservation Group.

Internation Projects: U.S. Technical Co-Leader for Wildlife in Managed Forests of India Project with Wildlife Institute of India, Habitat Futures Conferences with Ministries of Forests and Environment, British Columbia, Canada, Chief Wildlife Ecologist for Developing an Integrated and Sustainable Land Use Program for the Ussuri River Watershed of the Russian Far East and Northeastern China Revied forest management plans for U.K. and South Africa, contributed to ecological work in Mexico, Caribbean, Costa Rica, Ecuador, Germany.

1988 - 1990. Area Wildlife Ecologist, USDA Forest Service. Developed wildlife habitat guides and habitat classification system to integrate with timber types and plant associations, decision models and expert systems. Coordination with field offices, wildlife biologists, silviculturists, planners.

1985 - 1988. Wildlife Ecologist. Pacific Northwest Regional Office, USDA Forest Service. Member, Spotted Owl Environmental Impact Statement Interdisciplinary Team; conducted, devised assessment of population viability. Headed regional Old-Growth Development Program, wrote and initiated 5-year Action Plan. Coordinated 13 National Forests in spotted owl monitoring. Developed expert systems for viability assessment and species identification.

1984 - 1986. Computer Programmer. Consultant to the Perkin-Elmer Corporation, Biomedical Division.

1979 - 1984. Graduate Research Assistant. Doctoral study at Oregon State University: initiated and wrote Cooperative Agreement with USDA Forest Service to validate and improve a prediction model of wildlife-habitat relationships. Dissertation addressed coordination of timber harvest planning and operations; use of modeling in National Forest land management planning and project assessment; field ecology of bird communities.

1983 - 1984. Ecological Consultant. Analyzed bird survey data for USDI Fish and Wildlife Service and USDA Forest Service Old-Growth Research Program.

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1980 - 1981. Instructor, Department of Wildlife Management, College of Natural Resources, Humboldt State University. Created and taught upper division and graduate courses in Principles of Wildlife Ecology, Ecology of Wildlife Populations, Philosophy and Ethics of Natural Resources Science, Habitat Modeling in Management Decisions.

1981. Instructor with 3 others, Workshop on Application of Remote Sensing to Wildlife Habitat Inventory, Humboldt State University.

1978 - 1979. Biological Technician, Six Rivers National Forest, USDA Forest Service. Implemented Slump Pond Habitat Management Plan. Helped develop Wildlife-Habitat Relationships Program. Forest Geobased Information System.

Contract Ecologist, USDA Forest Service. Spotted owl and flammulated owl surveys. Developed maps of owl locations for timber sale Environmental Analyses. Devised and conducted wildlife and limnoligical studies of slump pond habitats. Wrote management plan for protecting pond habitats on Six Rivers National Forest.

AWARDS:

Oregon Wildlife Society Award for Outstanding Service for Wildlife Resources of Oregon. 1994.
Forest Ecosystem Management Assessment Team, USDA Forest Service. 1993.
Scientific Analysis Team, USDA Forest Service. 1993.
Honorary Member, The Wildlife Foundation of Khabarovsk, Russia. 1993.
1992 Conservationist of the Year, The Oregon Rivers Council.
Certificate of Appreciation, California Spotted Owl Technical Assessment Team. 1992.
Wildlife Publication Award for Monograph, The Wildlife Society. 1992.
Group Achievement Award, The Wildlife Society. 1991.

PROFESSIONAL ASSOCIATIONS:

Cooper Ornithological Society
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The Nature Conservance
The Wildlife Foundation of Khabarovsk, Russia
Ecological Society of America
Society for Conservation Biology
World Wildlife Fund
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American Association of Artificial Intelligence

PUBLICATIONS:

Marcot, B.G.; Murphy, D.D. In press. Population viability analysis and management. In: Szaro, R., ed. Biodiversity in Managed Landscapes: Theory and Practice. (Proceed. of conference 13-17 July 1992, Sacramento, CA.) Oxford Univ. Press.

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Marcot, B.G. 1977. Limnology, vegetation, and classification of slump ponds in northwestern California. M.S. Thesis, Humboldt State University, Arcata, CA.

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EDUCATION:

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PROFESSIONAL EXPERIENCE:

1985 - present. A. Starker Leopold Endowed Chair. University of California, Berkeley.

1980 - present. Professor, University of California, Berkeley.

1986 - 1990. Vice-chairman, Department of Forestry and Resource Management. University of California, Berkeley.

1974 - 1979. Professor, University of Michigan.

1971 - 1972, 1974. Chairman, Resource Ecology Program, University of Michigan.

1969 - 1974. Associate Professor, University of Michigan.

1966 - 1969. Assistant Professor, University of Michigan.

1965 - 1966. Acting Assistant Professor, University of California, Berkeley.

1963 - 1965. Field Investigator, Museum of Vertebrate Zoology, University of California, Berkeley.

1962 - 1963. Teaching Assistant, University of California, Berkeley.

Summer 1961. Summer Biologist, Arctic Health Research Center, Cape Thompson, AK.

1960 - 1962. Curatorial Assistant, Museum of Vertebrate Zoology, University of California, Berkeley.

Summer, 1960. General Assistant, Pacific Cooperative Water Pollution and Fisheries Research Laboratory.

1958 - 1960. Graduate Assistant, Oregon Cooperative Wildlife Research Unit.

PUBLICATIONS:

McCullough, D.R.; Weckerly, F.W.; Garcia, P.I.; Evett, R. Accepted. Factors influencing variability in herd composition counts. J. of Wildl. Manage.

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McCullough, D.R. 1964. Relationship of weather to migratory movements of black-tailed deer. Ecology 45(2):249-256.

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Fisheries, Wildlife and Range
USDA Forest Service, Southern Region

EDUCATION:

M.S. 1965. Louisiana State University. Wildlife Management.

B.S. 1964. Louisiana State University. Forestry.

PROFESSIONAL EXPERIENCE:

1984 - present. USDA Forest Service. Director of Fish, Wildlife and Range, Southern Region. Supervises operations and activities of 18 personnel engaged in professional, technical and clerical work concerned with Fisheries, Wildlife and Range program. Participates with the Regional Forester, Deputies and other staff in the formulation and establishment of regional, natural resource management policies and programs. Serves as consultant and authoritative expert to the Regional Forester, Deputies and other staff members on fish, wildlife habitat and range management. Evaluates compliance with policies, objectives and standards, overall effectiveness of operations and provides technical assistance to Region 8 Forest Supervisors.

1978 - 1981. USDA, Forest Service. Endangered Species Specialist, Washington, D.C. Formulated and recommended policies, plans, program, and standards of national scope for the FS endangered species program. Coordinated FS T&E program with outside agencies and groups. Reviewed policies, plans and standards recommended by other members of Chief's staff and field units. Made periodic field checks of FS operations to determine compliance with planned design and projected output. Provided technical leadership and guidance to field in all phases of T&E program. Chaired the USDA Endangered Species Working Group and International Wildlife subcommittee. Represented USDA on the International Convention Advisory Commission.

1975 - 1978. USDA Forest Service. Endangered Species Specialist, California. Recommended scientific leadership in the development of a Regional program for T & E species. Recommended Regional T & E policy, prepared guidelines and standards, directed workshops and provided training. Assisted Forest Supervisors and State Foresters of Hawaii and California in development and implementation of T & E species habitat management plans, design of studies and coordination of programs. Coordinated Regional T & E program with other agencies and groups.

1973 - 1975. USDA Forest Service. Forester (Wildlife). Florida. Designed surveys to evaluate critical habitat for endangered species; coordinated aerial bald eagle and osprey nesting surveys. Cooperated with several agencies and universities conducting endangered species research on the forests. Provided management recommendations for wildlife, including endangered species for three unit plans, one forest direction statement and two timber management plans.

1968 - 1973. USDA Forest Service. Forester (Wildlife). Cherokee National Forest. Administered wildlife and range program on the Cherokee National Forest. Worked closely with Tennessee Game and Fish Commission to raise cooperative habitat improvement program from $25 thousand to $100 thousand dollars. Gained considerable experience in trout stream improvement and evaluation of the effects of logging on streams.

Mar. 1968 - Oct. 1968. USDA Forest Service. Assistant District Ranger, Ouachita National Forest. Assistant District Ranger. Administered wildlife, range, timber and recreation programs. Emphasis on cattle-wildlife relationships.

1966 - 1968. USDA Forest Service. Forester (Wildlife). Shawnee National Forest. Wildlife biologist in charge of wildlife management activities on Shawnee National Forest. Administered cooperative habitat improvement program with Illinois State Wildlife Agency. Administered 3,000-acre greentree reservoir for waterfowl. Planned and supervised initial construction of a 2,000-acre addition to the reservoir.

1965 - 1966. USDA Forest Service. Forester. Illinois. Responsible for wildlife habitat improvement, recreation and administration and land acquisition. Land acquisition budget was approximately $1 million for the District.

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PROFESSIONAL ASSOCIATIONS AND AWARDS:

The Wildlife Society.
Society of American Foresters Chair, Fisheries and Wildlife Ecology Working Group (1979-1980).
Advisory Committees for: Virginia Tech Wildlife Department Mississippi State University Fish and Wildlife Department.
Board of Directors for the Georgia Wildlife Federation.
XI Sigma Pi. Honorary Forestry Fraternity
Research Assistant for Graduate Study
Quality Increase - 1981
Special Act Cash Award - 1986

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British Columbia Ministry of Forests

EDUCATION:

Ph.D. 1989. University of British Columbia. Course emphasis; philosophy of science, population biology, behavioural ecology.

M.Sc. 1983. University of British Columbia. Course emphasis; theoretical population biology and modeling, biometrics, behavioural ecology.

B.Sc. 1976. University of British Columbia. Course emphasis; nutrition, physiology, genetics, biometrics, wildlife management.

PROFESSIONAL EXPERIENCE:

1989 - present. Wildlife Research Ecologist, Research Branch, B.C. Ministry of Forests. Coordinate, direct, and conduct wildlife/forestry research on issues that are of provincial importance. Job involves obtaining required funding, hiring and managing personnel, purchasing equipment, logistics, design of methods, field work, data analysis, publishing results, academic duties, public presentations.

1980 - present. Director/Research Biologist, Flathead Grizzly Bear Research Project. Solicit funding from private and government sources, hiring and managing personnel, purchasing equipment, logistics, design of methods, snaring, immobilizing and radio tracking grizzly and black bears, vegetation sampling, behavior and activity sampling, data analysis, publishing results, academic duties, public presentations.

1986 - 1988. Partner/Research Biologist, Keystone Bio-Research. Logistics and design of methods, personnel management, snaring, net gunning, trapping, and helicopter darting elk, deer and moose. Conducting radio tracking, track transects, browse transects and aerial census, data analysis and report preparation.

1977 - 1980. Research Biologist. Hiring and managing personnel, purchasing equipment, logistics, design of methods, data analysis and report preparation. Trapping, immobilizing and radio tracking elk, mountain goats, and grizzly bears. Track counts, browse surveys, vegetation sampling, aerial, ground and interview population census for elk, moose, and mountain goats.

Adjunct Professor, Faculties of Forestry and Agriculture, University of British Columbia.

REFEREED JOURNAL PUBLICATIONS:

McLellan, B.N.; Hovey, F.W. 1993. The diet of grizzly bears in the Flathead drainage of Southeastern British Columbia. To be submitted to Canadian Journal of Zoology.

McLellan, B.N. 1989. Population dynamics of grizzly bears during a period of resource extraction development. I. Density and age/sex structure. Can. J. Zool. 67:1861-1864.

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SYMPOSIUM PUBLICATIONS:

McLellan, B.M.; Hovey, F.W. (in press) Development and preliminary results of partial-cut timber harvesting in a riparian area to maintain grizzly bear spring habitat values. In Morgan, K., ed. Ecology in Riparian Habitats.

McLellan, B.N.; Reiner, D. (in press) A review of bear evolution. Int. Conf. Bear Res. and Manage. 9:000-000.

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McLellan, B.N. 1992. Competition between black and grizzly bears as a natural population regulating factor. In: Keay, J.A., ed. Proc. of the Fourth Western Black Bear Workshop. USDA Tech. Rep. NPS/NRWR-93/12. Pp. 111-116.

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EDUCATION:

Ph.D. 1988. *University of Alberta. Zoology.*

M.S. 1981. Portland State University. Biology (Ethology).

B.S. 1974. Arizona State University. Zoology (Wildlife Biology).

B.A. 1970. University of Santa Clara. Philosophy

PROFESSIONAL EXPERIENCE:

1992 - *present. Research Biologist, McCallum Paquet Associates.*

1988. Adjunct Professor of Biology, Brandon University, Brandon, Manitoba.

1987 - present. Research Biologist, John/Paul & Associates.

1988. Lecturer, Brandon University.

1985 - 1987. *Wildlife Biologist, Canadian Wildlife Service.*

1984. Teaching Assistantship - Lecturer, General Ecology, Department of Zoology, University of Alberta, Edmonton.

1982 - 1987 Research Assistant, Boreal Institute for Northern Studies, Canadian Wildlife Service Wolf Ecology Project, Riding Mountain National Park, Manitoba.

1981 - 1982. *Canine Consultative Service, Portland, OR.*

1979 - 1981. Carpenter, Richard & Assoc., Portland, OR.

1975 - 1979. Graduate Assistant, Portland State University.

1973 - 1974. Independent Contractor: U.S. Bureau of Land Management Arizona Fish and Wildlife.

PROFESSIONAL ASSOCIATIONS:

American Association for the Advancement of Science
New York Academy of Science
Society for Conservation Biology
Canadian Society of Zoologists
The Wildlife Society of Canada
The American Society of Mammalogists
The Wildlife Society, Washington, D.C.

PUBLICATIONS:

Books and Chapters

Paquet, P.C.; Weaver, J. In prep. Behavioral ecology of grey wolves in the Rocky Mountains.

Clark, T.; Paquet, P.C.; Noss, R., eds. In prep. Conservation of large carnivores in the Rocky Mountains, North America. Conservation Biology. The Journal for the Society of Conservation Biology. Blackwell Scientific Publications, Inc. Cambridge, MA.

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Paquet, P.C. In press. A strategy for conservation of gray wolves in the Central Canadian Rocky Mountains. Proceedings of the Leon, Spain International Conference on Gray Wolves.

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McCallum, M.J.; Paquet, P.C. In prep. Special features in Yoho National Park, MT. Prepared for Parks Canada, Yoho National Park, B.C.

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University of Montana

EDUCATION:

Ph.D. 1982. Yale University. Forestry Wildlife Ecology.

M.S. 1977. Kansas State University. Wildlife Biology.

B.S. 1974. University of Minnesota. Wildlife Management.

PROFESSIONAL EXPERIENCE:

1993 - Present. University of Montana. Director, Wildlife Biology Program. Coordinate interdisciplinary group of 15 faculty with 325 undergraduate and 25 graduate students.

1984 - Present. University of Montana. Professor. Teach wildlife in School of Forestry and research on predators and prey in western Montana.

1985. Instructor: Taught part of a workshop on wildlife techniques at the Pakistan Forest Institute, Peshawar, Pakistan. U.S. Fish & Wildlife Service.

1983. Visiting Instructor: Taught Wildland Animal Dynamics and Wildlife Techniques in the College of Natural Resources. University of California, Berkeley.

1982. Teaching Assistant: Assisted teaching a wildlife ecology course in the School of Forestry and Environmental Studies. Yale University.

1982. Instructor. Taught the section on aging and sexing at a wildlife techniques workshop in Kanha National Park, India. U.S. Fish & Wildlife Service.

1978 - 1981. (Summers). Research Assistant: Conducted research on the effects of deer on nutrient cycling. Yale University.

1976. Assistant Instructor and Undergraduate Advisor: Taught a 3-credit course in Wildlife Techniques. Kansas State University.

1975 - 1976. Graduate Research Assistant: Research on the indirect effects of an herbicide (2, 4-D) on bobwhite. Kansas State University.

1974. Research Assistant: Assisted with moose studies on Isle Royale National Park. University of Minnesota.

PROFESSIONAL ASSOCIATIONS:

The Wildlife Society
Montana Chapter, The Wildlife Society
Northwest Section, The Wildlife Society
The Ecological Society of America
Fauna and Flora Preservation Society
Boone and Crockett Club
Society for Conservation Biology

TEACHING EXPERIENCE:

Survey of Wildlife Careers
Wildlife Research Techniques
Principles of Wildlife Biology
Mammal Conservation and Management
Seminar in Endangeered Species
Seminar: Decision Analysis in Wildlife
Wilderness Ecology
Wildlife Biotelemetry
Game Harvest Management
Review of Wildlife and Environmental Film

INTERNATIONAL EXPERIENCE:

Wildlife Techniques course, Kanha National Park, India.

Wildlife Techniques course, Pakistan Forest Institute, Peshawar.

Worked with graduate students on Tibetan Plateau, People's Republic of China.

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Worked with graduate students from India, Pakistan, People's Republic of China, Taiwan, Nepal, Sudan.

Chairman, International Affairs Committee, The Wildlife Society, 3 years.

PUBLICATIONS:

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North Carolina State University

EDUCATION:

Ph.D. 1977. University of Chicago. Department of Biology.

B.A. Carleton College. Environmental Studies.

PROFESSIONAL EXPERIENCE:

1985 - present. Associate Professor, Departments of Zoology and Forestry, North Carolina State University. Teach wildlife management, mammalogy, predator-prey relationships, advanced topics in mammals, animal community ecology.

1990 - 1991. Visiting Professor, University of Wyoming. Department of Zoology and Physiology.

1990 - present. Affiliate Faculty, Department of Biology, Colorado State University.

1979 - 1985. Assistant Professor, Department of Zoology and Forestry, North Carolina State University.

1982. Visiting Professor, Department of Zoology, Oulu University, Oulu, Finland. Taught population ecology and dynamics of northern mammals.

1978 - 1979. Visiting Assistant Professor, Department of Ecology, Ethology & Evolution, University of Illinois. Taught ethology of mammals, animal behavior lab, introduction to northern forest ecology, predator-prey relationships.

1978. Visiting Scholar, Department of Biology, University of Chicago.

1978. Lecturer, Biological Sciences, College Division, University of Chicago. Taught habitats and organisms.

1977. Lecturer, Biological Sciences, College Division, University of Chicago. Taught mammalogy.

1971. U.S. Fish & Wildlife Service. Technician for L. David Mech.

PUBLICATIONS:

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Powell, R.A. 1973. A model for raptor predation on weasels. J. Mammal. 54:259-263.

Powell, R.A. 1972. A comparison of populations of boreal red-backed vole (*Clethrionomys gapperi*) in tornado blowdown and standing forest. Can. Field-Natur. 86:377-379.

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EDUCATION:

Ph.D. 1977. Wildlife Ecology. Utah State University.

Ph.D. candidate 1973-74. Oregon State University.

M.S. 1973. Wildlife Biology. Utah State University.

B.S. 1969. Business Administration and Management. Indiana State University.

PROFESSIONAL EXPERIENCE:

1992 - present. Adjunct Professor, Department of Fish and Wildlife Resources, University of Idaho. Taught fish and wildlife population ecology, natural resources ecology.

1986 - 1992. Adjunct Associate Professor, Department of Fish and Wildlife Resources, University of Idaho. Taught wildlife management, introduction to wildlife biology, behavioral ecology and management, wildlife professions.

1985 - 1986. Associate Professor, Department of Fishery and Wildlife Biology, Colorado State University. Taught wildlife techniques, integrated resource management.

1980 - 1985. Assistant Professor, Wildlife Biology - Department of Zoology, Washington State University. Taught principles of wildlife management, wildlife ecology, wildlife techniques, waterfowl ecology and management, behavioral ecology.

1977 - 1980. Assistant Professor, Department of Wildlife and Fisheries Sciences, South Dakota State University. Taught wildlife management, ornithology, population ecology, nongame bird management.

1974 - 1977. Instructor and Teaching Assistant, Department of Wildlife Science, Utah State University.

1974 (summer). Instructor, Pacific University and the Malheur Environmental Field Station, Burns, OR. Taught waterfowl ecology and management.

PUBLICATIONS:

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Grimm, D.B.; Ratti, J.T.; Friesz, R. 1984. Effects of volcanic ash on food habits of burrowing owls at Moses Lake, Washington. Northwest Science. 59:40-44.

Ratti, J.T.; McCabe, T.R.; Smith, L.M. 1983. Morphological divergence between western grebe color morphs. J. Field Ornithology 54:424-426.

Hupp, J.W.; Ratti, J.T. 1983. A test of radio telemetry triangulation accuracy in heterogeneous environments. In Pincock D.G., ed. Proceedings Fourth International Conf. Wildlife Biotelemetry, Applied Microelectronics Institute and Technical University of Nova Scotia, Halifax. Pp. 31-46.

Ratti, J.T.; Smith, L.M.; Hupp, J.W.; Laake, J.L. 1983. Line transect estimates of density and the winter mortality of gray partridge. J. Wildl. Manage. 47:1088-1096.

Lebeda, C.S.; Ratti, J.T. 1983. Reproductive biology of Vancouver Canada geese on Admiralty Island, Alaska. J. Wildl. Manage. 47:297-306.

Smith, L.M.; Hupp, J.W.; Ratti, J.T. 1982. Habitat use and home range of gray partridge in eastern South Dakota. J. Wildl. Manage. 46:580-587.

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Smith, L.M.; Hupp, J.W.; Ratti, J.T. 1980. Reducing abandonment of nest-trapped gray partridge with methoxyflurane. J. Wildl. Manage. 44:690-691.

Ratti, J.T. 1979. Reproductive separation and isolating mechanisms between dark- and light-phase western grebes. Auk 96:573-586.

VanHorn, D.; Harrington, P.; Ratti, J.T. 1979. Preliminary results of surveys of the Vancouver Canada goose (*Branta canadensis fulva*) in Southeast Alaska. In Jarvis R.L.; Bartonek J.C., eds. Proceedings of management and biology of Pacific flyway geese. N.W. Sect. Wildlife Society, Portland. Pp. 310-315.

Ratti, J.T.; Timm, D.E. 1979. Migratory behvaior of Vancouver Canada geese: Recovery rate bias. In Jarvis R.L.; Bartonek J.C., eds. Proceedings of management and biology of Pacific flyway geese. N.W. Sect. Wildlife Society, Portland. Pp. 208-212.

Ratti, J.T.; Timm, D.E.; Anderson, D.R. 1978. Reevaluation of survival estimates for Vancouver Canada geese: Application of modern methods. Wildl. Soc. Bull. 6:146-148.

White, G.C.; Ratti, J.T. 1977. Estimation and testing of parameters in Richard's growth model for western grebes. Growth 41:315-323.

Ratti, J.T.; Timm, D.E.; Robards, F.C. 1977. Weights and measurements of Vancouver Canada geese. Bird-Banding 48:354-357.

Ratti, J.T.; Workman, G.W. 1976. Hunter characteristics and attitudes relating to Utah shooting preserves. Wildl. Soc. Bull 4:21-25.

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MARK L. SHAFFER

VICE PRESIDENT FOR RESOURCE PLANNING AND ECONOMICS
The Wilderness Society

EDUCATION:

Ph.D. School of Forestry and Environmental Studies. 1978. Duke University.

B.S. (Ed.) 1972. Indiana University of Pennsylvania.

PROFESSIONAL EXPERIENCE:

1991 - present. Vice President of the Wilderness Society for Resource Planning and Economics. Responsible for policy analysis and formulation for major national environmental organization. Supervise 13 professional researchers including ecologists and economists, GIS technical specialists and attorneys. Responsible for program development, fund raising, administration, personnel supervision.

1988 - 1991. Responsible for direct supervision and administration of 18 cooperative research units and two projects located at 20 major universities throughout the U.S. Supervise 35 Ph.D.s in a $9 million program. Units undertake a program of research in fish and wildlife management, conservation biology, and natural resource management.

1987 - 1988. Staff Specialist U.S. Fish and Wildlife Service, Office of International Affairs. Provided general staff support to Director on international wildlife conservation issues.

1985 - 1987. Senior Ecological Adviser, Agency for International Development. Provided technical expertise and profession guidance in creation of congressionally mandated program for biodiversity conservation in developing nations. Involved extensive coordination and liaison with virtually every U.S. governmental and non-governmental organization with interests in global conservation. Managed federal task force with 13 member agencies to develop their role in program, wrote two annual reports to Congress, drafted major concept paper outlining options for program staffing, budgeting, and implementation.

Staff Specialist, U.S. Fish and Wildlife Service, Office of Migratory Bird Management. Responsible for conservation issues, both domestic and foreign. Coordinated experts nationwide to assemble a list of unstable and declining migratory birds. Drafted Service's first plan for national nongame migratory bird management program intended to prevent endangerment of unstable and declining species. Principal Service staff working with national Marine Fisheries Service on resolution of Japanese fishing impacts on U.S. seabirds, Wrote Service position on selected legislation.

GOVERNMENTAL AFFAIRS, INVITED CONSULTATIONS:

Represented U.S. Government on official delegations including the Wetlands Convention, ASEAN Nations Conference on Science and Technology, First Conference on National Parks in Thailand.

Special Task Forces, Consultations: The Wildlife Society review of The Endangered Species Act; National Park Service's Task Force on Conserving Biodiversity in the National Parks; four AID missions in Asia and Central America on biodiversity program implementation; Special report to Office of Technology Assessment on state of knowledge in estimating population viability of wildlife species.

Consultant on specific endangered species issues for federal and state agencies (grizzly bear, California condor, black-footed ferret, spotted owl)

Technical and Program Review Committees for BLM, MMS, NPS, USFS.

Editorial Board for Conservation Biology, peer reviewer for NSF, Science, BioScience, American Naturalist, and others.

Past member, Board of Governors, Society for Conservation Biology.

PUBLICATIONS:

Shaffer, M.L. 1992. *Keeping the Grizzly Bear in the American West: A Strategy for Real Recovery*. The Wilderness Society, Washington, D.C. 17 p.

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Shaffer, M.L. 1992. Beyond the Endangered Species Act: Conservation in the 21st Century. 24 p.

Shaffer, M.L. 1991. Population viability analysis. In: Decker, D.J.; Krasny, M.E.; Goff, G.R.; Smith, C.R.; Gross, D.W., eds. Challenges in the Conservation of Biological Resources: A Practitioner's Guide. Westview Press, Boulder, CO. Pp. 107-118.

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Harris, R.B.; Clark, T.W.; Shaffer, M.L. 1989. Estimating extinction probabilities for isolated black-footed ferret populations. In: Seal, U.S.; Thorne, E.T.; Bogan, M.A.; Anderson, S.A., eds. Reproduction Biology of the Black-footed Ferrets and Small Population Biology as They Relate to Conservation. Yale University Press, New Haven, CT. Pp. 69- 82.

Maguire, L.A.; Clark, T.W.; Crete, R.; Cada, J.; Groves, C.; Shaffer, M.L.; Seal, U.S. 1988. Black-footed ferret recovery in Montana: A decision analysis. Wildl. Soc. Bull. 16:111- 120.

Shaffer, M.L. The minimum viable population problem: Coping with uncertainty. In: Soulè, M.E., ed. Viable Populations for Conservation. Cambridge Univ. Press, Cambridge. Pp. 69-86.

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Samson, F.B.; Perez-Trejo, F.; Salwasser, H.; Rugglero, L.F.; Shaffer, M.L. 1985. On determining and managing minimum population size. Wild. Soc. Bull. 13:425-433.

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Erwin, R.M.; Geissler, P.H.; Shaffer, M.L.; McCrimmon, Jr., D.A. 1985. Colonial bird monitoring: A strategy for regional and national evaluation. In: McComb, W., ed. Proceedings - Workshop on Management of Nongame Species and Ecological Communities. Univ. of Kentucky, Agri. Exper. Sta., Lexington.

Shaffer, M.L.; Samson, F.B. 1985. Population size and extinction. A note on determining critical population sizes. *American Naturalist* 125(1):144-152.

Shaffer, M.L. 1983. Determining minimum viable population sizes for the grizzly bear. Int. Conf. Bear Res. and Manage. 5:133-139.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. BioScience 31:131-134.

Shaffer, M.L. 1979. Behavior of the European wild boar in Great Smoky Mountains National Park. In: Linn, R.M., ed. Proceedings First Conference on Scientific research in the National Parks. Vol. 1. NPS Trans. and Procds. Ser. No. 5. USDI, Washington, D.C. Pp. 357-364. (Presented at the First Conference on Scientific Research in the National Parks, Nov. 9-12, 1976, New Orleans, LA.

Shaffer, M.L. 1975. Computer simulation of the effects of roadways on the frequency and extent of forest fires. In: Meadows, J.; Bare, B.; Ware, K.; Row, C., eds. Systems Analysis and Forest Resources Management. SAF, Bethesda, MD. Pp. 327-335. (Presented at: Workshop on Systems Analysis and Forest Resource Management, Aug. 10-13, 1975, Athens, GA.

Sullivan, A.L.; Shaffer, M.L. 1975. Biogeography of the Megazoo. Science 189:13-17.

Murphy, J.A.; Drory, A.; Shaffer, M.L., eds. 1974. World Data Center A. Oceanography. Catalog of Ascensioned Publications, Supplement No. 6. NOAA, Washington, D.C.

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CHRISTOPHER C. SMITH

PROFESSOR
Kansas State University

EDUCATION:

B.A. University of Colorado. 1960.

M.A. University of Washington. 1963.

Ph.D. University of Washington. 1965.

PROFESSIONAL EXPERIENCE:

Professor, Kansas State University, 1981-present.

Associate Professor, Kansas State University, 1970-1981.

Assistant Professor, University of Missouri, 1968-1970.

Teaching Faculty, Fern Mountain Field Ecology Program, Summer, 1980-1981.

Visiting Scientist, Museum of Northern Arizona, 1978-1979.

Teaching Faculty, Organization for Tropical Studies, Summer, 1971.

National Research Council, Postdoctoral Research Assistantship, Smithsonian Tropical Research Institute, 1967-1968.

Assistant Professor, Fish University, 1965-67.

COURSES TAUGHT AT KSU:

Principles of Biology Recitations and Laboratory, Organismic Biology, Ecology and Ecology Laboratory, Honors Seminar: "The Evolution of Human Nature," Interim Semester Field Courses, Mammalogy, Population Biology, Evolution and Population Genetics, Evolutionary Ecology.

PROFESSIONAL ASSOCIATIONS:

American Society of Naturalists
Ecological Society of America
Society for the Study of Evolution
American Society of Mammalogists
American Association for the Advancement of Science
Botanical Society of America
Sigma Xi
Phi Beta Kappa
Phi Sigma Biological Honarary Society

PUBLICATIONS:

Smith, C.C. 1993. Foraging and flocking behavior. In Experiments to Teach Ecology, Beiswenger J.M., ed. Ecological Society of America, Tempe, AZ, Pp. 111-154.

Gali, H.U.; Smith, C.C. 1992. Effect of silicon supply on growth, fertility and mineral composition of an annual brome, *Bromus secalinus* L. (Gramineae). American Journal of Botany 79:

Gali-Muhtasib, H.; Smith, C.C.; Higgins, J.J. 1992. The effect of silica in grasses on the feeding behavior of the prairie vole *Microtus ochrogaster*. Ecology 73:1724-1729.

Smith, C.C. 1992. Testing issues of foraging and flocking behavior. In Tested studies for laboratory teaching, Volume 13. Goldman C.A., ed. Proceedings of the 13th Workshop/Conference of the Association for Biology Laboratory Education (ABLE), Pp. 1-17.

Monzyk, F.R.; Smith, C.C. 1991. Fox squirrel rate of seed removal in comparison to that of nocturnal animals. Trans. Kansas Acad. Sci. 94:30-32.

Smith, C.C.; Hamrick, J.L.; Kramer, C.L. 1990. The advantage of mast years for wind pollination. American Naturalist 136:154-166.

McGinley, M.A.; Smith, C.C.; Elliott, P.F.; Higgins, J.J. 1990. Morphological constraints on seed mass in lodgepole pine. Functional Ecology 4:183-192.

Evans, E.W.; Smith, C.C.; Gendron, R.P. 1989. Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. Oecologia 78:220-230.

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Smith, C.C.; Hamrick, J.L.; Kramer, C.L. 1988. The effects of stand density on frequency of filled seed and fecundity in lodgepole pine (*Pinus contorta* Dougl.). Can. J. For. Res. 18:453-460.

Kraus, K.E.; Smith, C.C. 1987. Fox squirrel use of prairie habitats in relation to winter food supply and vegetation density. Prairie Naturalist 19:115-120.

Stapanian, M.A.; Smith, C.C. 1986. How fox squirrels influence the invasion of prairies by nut-bearing trees. J. Mamm. 67:326-332.

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Smith, C.C. 1978. The structure and function of the vocalizations of the tree squirrels (*Tamiasciurus*). J. Mammalogy 59:767-782.

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Bradford, D.F.; Smith, C.C. 1977. Seed predation and seed number in *Scheelea* palm fruits. Ecology 58:667-673.

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Smith, C.C. 1976. When and how much to reproduce: the trade-off between power and efficiency. Amer. Zool. 16:763-764.

Smith, C.C. 1975. The coevolution of seeds and seed predators. In Gilbert L.E.; Raven P.H., eds. Coevolution of animals and plants. Univ. Texas Press, Austin. Pp. 53-77.

Smith, C.C.; Fretwell, S.D. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499-506.

Smith, C.C. 1973. The distribution of energy into sexual and asexual reproduction in wild strawberries (*Fragaria virginiana*). Proceedings of the Third Midwest Prairie Conference. pp 55-60.

Smith, C.C.; Follmer, D. 1972. Food preferences of squirrels. Ecology 53:82-91.

Smith, C.C. 1970. The coevolution of the pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40:349-371.

Smith, C.C. 1968. The adaptive nature of social organization in the genus of tree squirrels (*Tamiasciurus*). Ecological Monographs 38:31-63.

Smith, C.C. 1963. First breeding record of the spotted owl in British Columbia. Conder 65:440.

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RICHARD D. TABER

AFFILIATE PROFESSOR
University of Montana

EDUCATION:

Ph.D. 1951. University of California, Berkeley. Zoology.

M.S. 1949. University of Wisconsin, Madison. Biology.

A.B. 1942. University of California, Berkeley. Zoology.

PROFESSIONAL EXPERIENCE:

1986 - present. Affiliate Professor, School of Forestry, University of Montana, Missoula, and Cooperator, Montana Cooperative Wildlife Research Unit.

1986 - present. Professor of Forest Zoology and Wildlife Science, Emeritus, University of Washington, Seattle.

1968 - 1985. Professor of Forest Zoology and Wildlife Science, University of Washington, Seattle; member, Institute of Environmental Studies.

1967 - 1968. Professor Wildlife Biology; Director, Center for Natural Resources Research, University of Montana.

1963 - 1964. Fulbright Research Professor, Zoology, West Pakistan Agricultural University, Lyallpur.

1956 - 1967. Assistant Professor to Professor, Forestry/Wildlife Biology; Assistant Leader, Cooperative Wildlife Research Unit; and Associate Director, Montana Forest and Conservation Experiment Station, University of Montana.

1955 - 1956. Acting Assistant Professor, Zoology; University of California, Berkeley.

1948 - 1955. Research Zoologist, California Forest and Range Experiment Station.

1946 - 1948. Conservation Aide, Wisconsin Conservation Department.

1942 - 1948. Commissioned Officer, U.S. Marine Corps.

1941 - 1942. Student Biologist, California Department of Fish and Game.

HONORS AND AWARDS

1958. Honorable Mention, for Best Publication by the Wildlife Society

1964-1965. Guggenheim Fellow, for work on Man and Wildlife in the Indus Valley

1968. Fellow, American Institute of Biological Sciences (AIBS)

1987. Wallmo Award from Western Deer Biologists, for research and teaching

1988. Einarsen Award, from Northwest Section, the Wildlife Society, for professional contributions

1990. Fellow, American Association for the Advancement of Sciences (AAAS)

PROFESSIONAL ASSOCIATIONS:

Wildlife Society (Pres. N.W. Sec., Comm. on Wildlife Techniques, Comm. on Position Papers, Editorial Referee, Grizzly Recovery Plan Rev. Comm.)
American Society of Mammalogists (Editorial Referee)
American Institute of Biological Sciences (Visiting Scientist Program)
American Association for the Advancement of Science
International Union of Forestry Research Organizations

PROFESSIONAL SERVICE (OTHER THAN PUBLICATIONS):

1952. Consultant for chaparral ecology, Arizona Game Commission

1956. Arctic Research Laboratory, Point Barrow, on lemming ecology study under F.A. Pitelka

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1960. American Specialist (Forest-Wildlife Relations) in West Germany, Poland, and Czechoslovakia, for U.S. Department of State.

1961. Invited Participant (w/R.S. Hoffmann) Ecol. Soc. Corvallis, on Terrestrial Vertebrate Biogeography of the Pacific Northwest

1964. Visiting Lecturer, Pakistan Forest Institute, Peshawar.

1964. American Specialist (Forest-Wildlife Relations) in Poland for the U.S. Department of State

1965. Atomic Energy Commission, Ecology Program, to confer on mule deer studies at Colorado State University

1968. Organizer, editor: Symp. on Coniferous Forests of the Northern Rocky Mountains, University of Montana

1968-1973. Visiting Consultant, West Pakistan, for the Smithsonian Institution

1970-1974. U.S. Peace Corps, to confer on programs of wildlife biology and conservation in Chile

1970-1980. City of Seattle, Department of Lighting, to design and supervise a biotic survey of Ross Lake Basin and to advise on mitigation and compensation

1971. Conference Summarizer, AAAS Conf. on Co-Action Among Natural Resource Biologists, sponsored by American Soc. of Range Mgmt., University of Wyoming, Laramie

1971. Invited participant, IUCN Conf. on Vicuna, Lima, Peru

1972. Visiting Lecturer, four-day short course on Population Dynamics for Colorado State Wildlife Research Group

1974. Invited participant, 3rd Internat. Cat Symposium, Seattle

1974. Texas A & M, speaker on Wildlife Research in Washington

1974. Yale School of Forestry, speaker on Forestry and Wildlife in Pacific Northwest

1975. Nominated Expert for Co-option/Consultation for Appointments, Professors, Department of Zoology, University of Agriculture, Lyallpur (Faisalabad) Pakistan

1976. North Amer. Wildlife Conf., Technical Session Chrm.

1977-Present. Member, Endangered Deer Group, International Union for the Conservation of Nature, (IUCN)

1977. U.S. Forest Service, Ft. Collins, workshop on Range Communities and Wildlife Conservation

1978. Elk Habitat Conf., Univ. Wyoming, Laramie, moderator

1979. Yale School of Forestry, U.S. Fish and Wildlife Service Workshop on Human Aspects of Wildlife Conservation, New Haven, Conn.

1980. U.C. Conf. on Cumulative Effects of Forest Management, June.

1980. Pakistan Forest Institute, Nov., workshop on Wildlife Mgmt. in Developing Countries

1981. National Research Council Working Group on Fish and Wildlife Issues

1982. Chairman, Working Party on Wildlife Gene Conservation International Union of Forestry Research Organizations (IUFRO)

1984-Present. Consultant, Taiwan (Republic of China) on re-introduction of Formosan Sika Deer and Development of national conservation strategy

1986. Invited participant, V International Snow Leopard Symposium, Srinagar, Kashmir, India. Lecturer, Wildlife Institute of India

1986. Invited participant, V Conference on World Conservation Strategy, Ottawa, Canada

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1990. Member, Ethnozoology Group, International Union for the Conservation of Nature Member, Technical Comm., Wilderness Society Greater Yellowstone Ecosystem Project

1992. Principal Investigator: Mammals of Taiwan, with support of Pacific Cultural Foundation, Taipei

PUBLICATIONS:

Taber, R.D. 1990. Is Land A Commodity: Review of Agricultural and Environmental Policies-Opportunities For Integration. Publ. by Organization for Economic Cooperation and Development, Washington, D.C. In: Western Wildlands 16(2):40-41, 44.

Pei, Chyi-Jai; Ying Wang; Taber, R.D. 1988. Taiwan mammals and conservation concerns. Abstr. Symp. on Asian Pacific Mammalogy, Beijing, P.R.C., July.

Taber, R.D. 1988. Long-term research in snow leopard conservation. In: Freeman, H., ed. Proc. Fifth International Snow Leopard Symposium. Int. Snow Leopard Trust and Wildlife Institute of India. Pp. 256-259.

Raedeke, K.J.; Taber, R.D.; Paige, D.K. 1988. Ecology of large mammals in riparian systems of Pacific Northwest forests. In: Raedeke, K.J., ed. Riparian Wildlife and Forestry Interactions. Contribution 59, Institute of Forest Resources, University of Washington, Seattle. Pp. 113-132.

Taber, R.D.; Raedeke, K.J. 1987. The management of *Cervus* in North America. In: Wemmer, C., ed. Biology and Management of *Cervidae*. Smithsonian Institution Press. Washington, D.C. Pp. 568-577.

Merrill, E.; Raedeke, K.; Knutson, K.; Taber, R. 1986. Elk recolonization and population dynamics in the northwest portion of the Mount St. Helens Blast Zone. In: Keller, S.A.C., ed. Symp. Proceed., Mt. St. Helens, 5 years later. Eastern Wash. Univ. Press, Cheney, WA. Pp. 359-368.

McCorquodal, S.; Raedeke, K.; Taber, R.D. 1986. Elk habitat use patterns in the shrub-steppe of Washington. Jour. Wildl. Manage. 50(4):644-669.

Taber, R.E.; Raedeke, K.J. 1985. Do cougars reduce hunter harvest of black-tailed deer in Washington State? Royal Society of New Zealand, Bulletin 22:49-50.

Raedeke, K.J.; Raber, R.D. 1985. Black-tailed deer population regulation through antlerless hunts in western Washington. Symposium on Game Harvest Management. Texas Tech. Press. Pp. 139-143.

Taber, R.D.; West, S.D. 1984. Biological processes in the control of risk tree species on rights-of-way in forested mountains: Pacific Northwest. In: Crabtree, A., ed. Third International Symposium on Environmental Concerns in Rights-of-Way Management, San Diego, Miss. State U. Press. Pp.410-415.

Taber, R.D. 1983. Toward the progress of wildlife conservation in North America. Trans. North American Wildlife and Natural Resources Conf. 48:468-472.

Taber, R.D. 1983. Wildlife conservation in the urban/rural interface. In: Bradley, G., ed. Proc. Conf. on the Urban/Forest Interface. Univ. Washington, Seattle, Pp. 109-111.

Miller, S.D.; Taber, R.D.; Raedeke, K.J.; Rottmann, J. 1983. Endangered mammals of Chile: status and conservation. Biol. Cons. 25:335-352.

Taber, R.D. 1982. Review: Mule and Black-tailed Deer of North America. Walmo, O.C., ed. 1981. Science V217; No. 4563:926.

Taber, R.D.; Raedeke, K.J.; McCaughran, D. 1982. Population characteristics. In: Thomas, J.; Toweill, D., eds. Elk of North America. Stackpole. Pp. 279-300.

West, S.D.; Taber, R.D.; Anderson, D.A. 1981. Wildlife in sludge-treated plantations. In: Bledsoe, C.S., ed. Municipal sewage waste application to lands in the Pacific Northwest. Proceedings of a symposium, University of Washington, Seattle, Pp. 115-122.

Taber, R.D. Lee, R.G.; West, S.D.; Raedeke, K.J.; de Calesta, D. 1981. Wildlife management in the mesic-temperate forest of Washington and Oregon. In: Proc. XVII, UIFRO World Conf. Sept. Kyoto, Japan. Pp. 575-587.

Taber, R.D.; West, S.D.; Raedeke, K.J. 1981. Some cumulative effects of forest management on wildlife. In: Helms, J., ed. Cumulative Effects of Forest Management on California Watersheds, Edgebrook Conf., Univ. California, Berkeley, August, 1981.

Taber, R.D. 1980. Review: Brokaw, H.P. 1976. Wildlife and America. Science 208(4442):390-391.

Taber, R.D.; Raedeke, K.J. 1980. Mechanisms of population regulation in western Washington forests for *Cervus* and *Odocoileus* in Proceedings V Union of Game Biologists, Dublin, Ireland.

Hanley, T.A.; Taber, R.D. 1980. Selective plant species inhibition by elk and deer in three conifer communities in western Washington. Forest Science 26(1)97-107.

Schoen, J.W.; Thornburg, G.N.; Taber, R.D. 1980. Ungulate habitat selection determined by location telemetry. 2nd International Conference on Wildlife Biotelemetry, Laramie, WY, July, 1979.

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Zasoski, R.J.; Taber, R.D. 1980. Heavy metal transfer to plants and rodents. In: Edmonds, R.L.; Cole, D.W., eds. Use of Dewatered Sludge as an Amendment for Forest Growth: Management and Biological Assessments. Vol. III. Bull. No. 3, Center for Ecosystem Studies, College of Forest Resources, University of Washington, Seattle. Pp. 70-74.

Taber, R.D.; Raedeke, K.J. 1979. Population dynamics. In: Wildlife Conservation. The Wildlife Society, Washington, D.C. Pp. 98-106.

Taber, R.D. 1979. Original wildlife of the Columbia Basin: changes over time. In: Dyer, P., ed. Water Rights for Fish and Wildlife. Published by Inst. for Env. Studies, Univ. Washington and Env. Res. Center, Washington State University. Pp. 71-88.

Hanley, T.A.; Taber, R.D. 1979. The black-tailed deer and forest succession in the Pacific Northwest. In: Wallmo, O.D.; Schoen, J.W., eds. Sitka Black-tailed Deer: Proceedings of a conference in Juneau, AK. USDA Forest Service, Alaska Region, in cooperation with the State of Alaska Department of Fish and Game. Series No. R10-48. Pp. 33-52.

Miller, S.; Rottmann, J.; Taber, R.D. 1978. The rare and endangered mammals of Chile and their conservation. 2nd International Theriological Congress, Bruno, Czechoslovakia. Abstract.

Hett, J.; Long, J.; Schoen, J.; Taber, R.D. 1978. Forest management policies and elk summer carrying capacity in the *Abies amabalis* forest, western Washington. Environmental Management 2(6):561-566.

Taber, R.D. 1977. Mammalian wildlife associated with sludge applications with particular emphasis on voles. In: Edmonds, R.L.; Cole, D.W., eds. Use of Dewatered Sludge as an Amendment for forest growth: Management and Biological Assessments. Vol. II. Bull. No. 2, Center for Ecosystem Studies, College of Forest Resources, University of Washington, Seattle.

Black, H.C.; Taber, R.D. 1977. Mammals in western coniferious forest ecosystems: an annotated bibliography. Bull. No. 2, Coniferous Forest Biome, Ecosystem Analysis Studies, U.S. International Biological Program. Univ. Washington, College of Forest Resources. IV+199 p.

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REPORT

Belowground carbon trade among tall trees in a temperate forest

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- Figures & Data
- Info & Metrics
- eLetters
- PDF

Carbon trading between adult trees

Competition between individual plants for resources is well known, but sharing of resources may also occur. Klein *et al.* observed tree-to-tree carbon shuttling between roots of tall trees in a mixed temperate forest in Switzerland (see the Perspective by van der Heijden). By applying stable carbon isotope labeling to individual tree canopies, they show that up to 40% of the carbon in the fine roots of one individual may be derived from photosynthetic products of a neighbor. Carbon transfer of this kind, mediated by plant-associated fungi, or mycorrhizae, in the soil, has been reported on a smaller scale in seedlings, but not before in trees.

Science, this issue p. 342; see also p. 290

Abstract

Forest trees compete for light and soil resources, but photoassimilates, once produced in the foliage, are not considered to be exchanged between individuals. Applying stable carbon isotope labeling at the canopy scale, we show that carbon assimilated by 40-meter-tall spruce is traded over to neighboring beech, larch, and pine via overlapping root spheres. Isotope mixing signals indicate that the interspecific, bidirectional transfer, assisted by common ectomycorrhiza networks, accounted for 40% of the fine root carbon (about 280 kilograms per hectare per year tree-to-tree transfer). Although competition for resources is commonly considered as the dominant tree-to-tree interaction in forests, trees may interact in more complex ways, including substantial carbon exchange.

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GEOGRAPHIC AND HOST RANGE OF THE NEMATODE *SOBOLIPHYME BATURINI* ACROSS BERINGIA

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ABSTRACT: The nematode *Soboliphyme baturini* Petrov, 1930, was found to represent a single species with a relatively broad geographic range across Beringia and northwestern North America on the basis of the assessment of molecular sequence data for adult and juvenile parasites. Refuted are hypotheses suggesting that several cryptic species could be partitioned either among an array of mustelid definitive hosts or across the vast region that links North America and Eurasia. Host specificity for this species is examined on the basis of a comprehensive list for definitive hosts, derived from new field surveys and existing literature for *S. baturini*. Only 5 mustelids (*Gulo gulo*, *Martes americana*, *M. caurina*, *M. zibellina*, and *Neovison vison*) appear to have significant roles in the life history, persistence, and transmission of this nematode. *Soboliphyme baturini* readily switches among *M. americana*, *M. caurina*, *Mustela erminea*, or *N. vison* at any particular locality throughout its geographic range in North America, although *Martes* spp. could represent the source for nematodes in a broader array of mustelids. Molecular analyses (243 base pairs of mitochondrial gene nicotinamide dehydrogenase [ND4]) suggest that hypotheses for host specificity across an array of mustelid definitive hosts are not supported. The life cycle of *S. baturini* is explored through a review of diet literature for 2 marten species, *M. americana* and *M. caurina*, and other mustelids across the Holarctic. Shrews (Soricomorpha: Soricidae) comprise >8% of prey for these species of *Martes*, suggesting their putative role as paratenic hosts. Juvenile nematodes found in the diaphragms of soricids are genetically identical to adult *S. baturini* found in the stomachs of mustelids at the same locations in both Asia and North America, corroborating a role in transmission for species of *Sorex*.

Establishing the roles for each participant in a parasite's life cycle is essential to interpreting ecology, epidemiology, distribution, and phylogeographic history. Hosts that are components of the life cycle can be defined as definitive (parasite achieves sexual maturity), intermediate (parasite develops, but does not reach sexual maturity), and paratenic (parasite undergoes no development stages, but might be transported from one trophic level to another) (Roberts and Janovy, 2005). Hosts can also be defined as incidental, when the parasite fails to reach sexual maturity. In this case, the host is unnecessary to the parasite life cycle and, therefore, could be insignificant to a parasite's evolutionary past. On the other hand, definitive hosts can have long-term coevolutionary relationships with their parasites, or the host/parasite relationship could be acquired through host switching (e.g., Brooks and McLennan, 1993; Hoberg, 2005). Recent relationships from host switching could be the result of ecological fitting (resource tracking), in which the parasite is tracking a resource in the host rather than the host itself (Kethley and Johnston, 1975; Janzen, 1985; Brooks et al., 2006).

Significant movements of species caused by the dynamic geologic events of the Pleistocene might have brought together new sets of potential hosts and increased the incidence of host colonization (Hoberg and Brooks, 2007). Hence, determinants of host associations and their relationship to host specificity can be a complex phenomenon (Brooks et al., 2006). Molecular perspectives have proved key to revealing such complexity, especially in dynamic ecological situations such as those that existed in high latitudes over the past 2 million yr (Cook et al., 2005).

Evolutionary roles for a spectrum of potential and actual hosts, however, might be unclear for nematode parasites when there is difficulty in distinguishing minute morphological differences between species (cryptic species) or when trying to link together adult and juvenile forms. Juveniles are often difficult to identify to species because of undeveloped morphological characters essential to diagnosis (e.g., Jenkins et al., 2005). In these cases, molecular identification is necessary when trying to match juveniles in intermediate and paratenic hosts with adult nematodes in definitive hosts (McKeand, 1998).

Soboliphyme baturini Petrov, 1930, is a stomach-dwelling nematode and member of the monotypic Soboliphymatidae, Dioctophymidea (Karmanova, 1986). A complex life cycle characterizes *S. baturini*, with adult nematodes maturing in the stomach of the definitive host and females then releasing eggs that are shed in feces and deposited in the soil. In the leaf litter, the eggs are consumed by the intermediate host, enchytraeid oligochaetes, where they hatch, and the resulting juveniles develop to the infective third juvenile stage (J_3) and are later transmitted to mammals (Karmanova, 1986). Soricomorphs and rodents feed on these oligochaetes and could serve as paratenic hosts by bridging the trophic gap between mustelid and oligochaete, or the definitive host might consume enchytraeids directly and become infected by the nematode (Karpenko, 1985; Karpenko et al., 1998, 2007). Adult *S. baturini* can survive in the definitive host for up to 20 mo; therefore, annual cohorts could overlap, leaving the hosts constantly infected (Karmanova, 1986).

Over 50 mammal species and subspecies are recognized hosts for *S. baturini* (Appendix); however, Kontrimavichus (1985) suggested that not all of these are necessary to the life cycle. For example, felids and canids are incidental hosts, meaning the juveniles can survive in the host but fail to reach sexual maturity (Karmanova, 1986). More specifically, *S. baturini* is most commonly found in sable (*Martes zibellina* (Linnaeus)), American marten (*Martes americana* (Turton)), and Pacific marten (*Martes caurina* (Merriam)) and less frequently in ermine (*Mustela erminea* Linnaeus), wolverine (*Gulo gulo* (Linnaeus)), and mink (*Neovison vison* (Schreber)) (Petrov, 1930; Price, 1930; Shimakura and Odajima, 1934; Bezdek, 1942; Morgan, 1943; Schmidt and Kinsella, 1965; Swartz, 1968; Kontrimavichus, 1985; Karmanova, 1986; Sato et al., 1999; Rusin et al., 2003; Zarnke et al., 2004).

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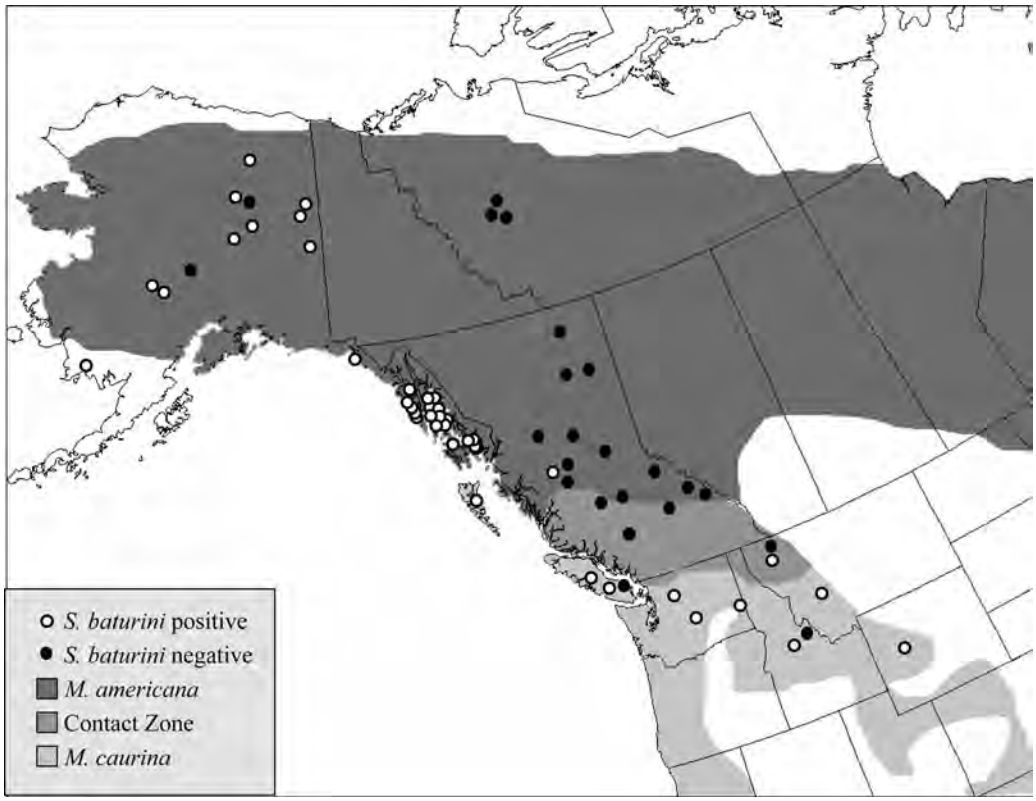

FIGURE 1. The geographic distributions of *M. caurina* and *M. americana* (modified from Hall, 1981) are overlapped with historic localities and survey results from this study for *S. baturini*. Admiralty and Kuiu Islands are the only islands known to support *M. caurina* in southeast Alaska. White dots represent occurrences of *S. baturini*. Black dots refer to necropsies of mustelids that were negative for *S. baturini*.

In North America, *S. baturini* is thought to be limited largely to the Pacific coast, with an eastward range extension to the southern Rocky Mountains. The southern range of this nematode coincides with the distribution of *M. caurina*, but intensive surveys need to be completed from southern and central British Columbia southward to northern New Mexico and northern California to adequately define this distribution. Further north, the nematode's distribution also includes the extreme western range of *M. americana* in southeast Alaska along the coast and in interior Alaska (Fig. 1). Occurrence of this nematode in *M. americana* apparently reflects 2 episodes of host switching (Koehler, 2006) in the Holocene, when *M. americana* expanded its range westward into both interior and coastal Alaska (Small et al., 2003).

Soboliphyme baturini is a prime candidate for studies that use molecular techniques to address the role of paratenic hosts in transmission and in exploring associations with definitive hosts. Worldwide host surveys over the past 76 yr resulted in recognition of a variety of potential definitive, intermediate, and paratenic hosts; yet, the roles that each of these host species played in the evolution of this nematode remain unclear (Fig. 2; Appendix). Additionally, the specifics of the life cycle of *S. baturini* have yet to be completely deduced, including the role of shrews as paratenic hosts and designation of the potential host species as either definitive or incidental.

In this study, the distribution of *S. baturini* was assessed with the use of new and historical data. Additionally, the following questions are explored. First, does *S. baturini* represent a single widespread species, or is there evidence for cryptic species partitioned across 5 mustelid hosts (i.e., *M. americana*, *M. caurina*, *M. zibellina*, *M. erminea*, and *N. vison*)? Second, are soricomorphs paratenic hosts of *S. baturini*? These hypotheses are the foundation for assessing the life history and distribution of *S. baturini*.

METHODS AND MATERIALS

In conjunction with the Beringian Coevolution Project (Hoberg et al., 2003; Cook et al., 2005), adult and juvenile *S. baturini* were obtained from 21 geographic sites across eastern Siberia and the Pacific Northwest (Table I). Adult nematodes from North American localities were acquired through necropsies of 756 salvaged mustelid carcasses from commercial trappers, including 460 *M. americana*, 124 *M. caurina*, 59 *Martes pennanti* (Erxleben), 70 *M. erminea*, 40 *N. vison*, 2 *Taxidea taxus* (Schreber), and 1 *G. gulo* (Table I). Of this total, 286 carcasses from interior British Columbia (n = 231), central Northwest Territories (n = 45), and Montana and Idaho (n = 10) (Table I) were studied to refine the eastern boundary of this nematode. Additional adult and juvenile specimens were obtained through collaborative efforts with other scientists (Appendix). Unpublished records from the U.S. National Parasite Collection (USNPC; USDA, Beltsville, Maryland) and from the University of Alaska Museum (AF; Fairbanks, Alaska) were also included. Specimens of adult *S. baturini* in stomachs of mustelids or J_3 of presumptive *S. baturini* in diaphragms of soricids were preserved in 70 or 95% ethanol and stored at −20 C before analysis. Each specimen was subsampled, with the midsection of the body being reserved for molecular sequencing, and the head and tail of individual adults or J_3 were archived as physical vouchers deposited in the Museum of Southwestern Biology (University of New Mexico, Albuquerque, New Mexico) (Table II).

Total genomic DNA was extracted from the midsections of individual

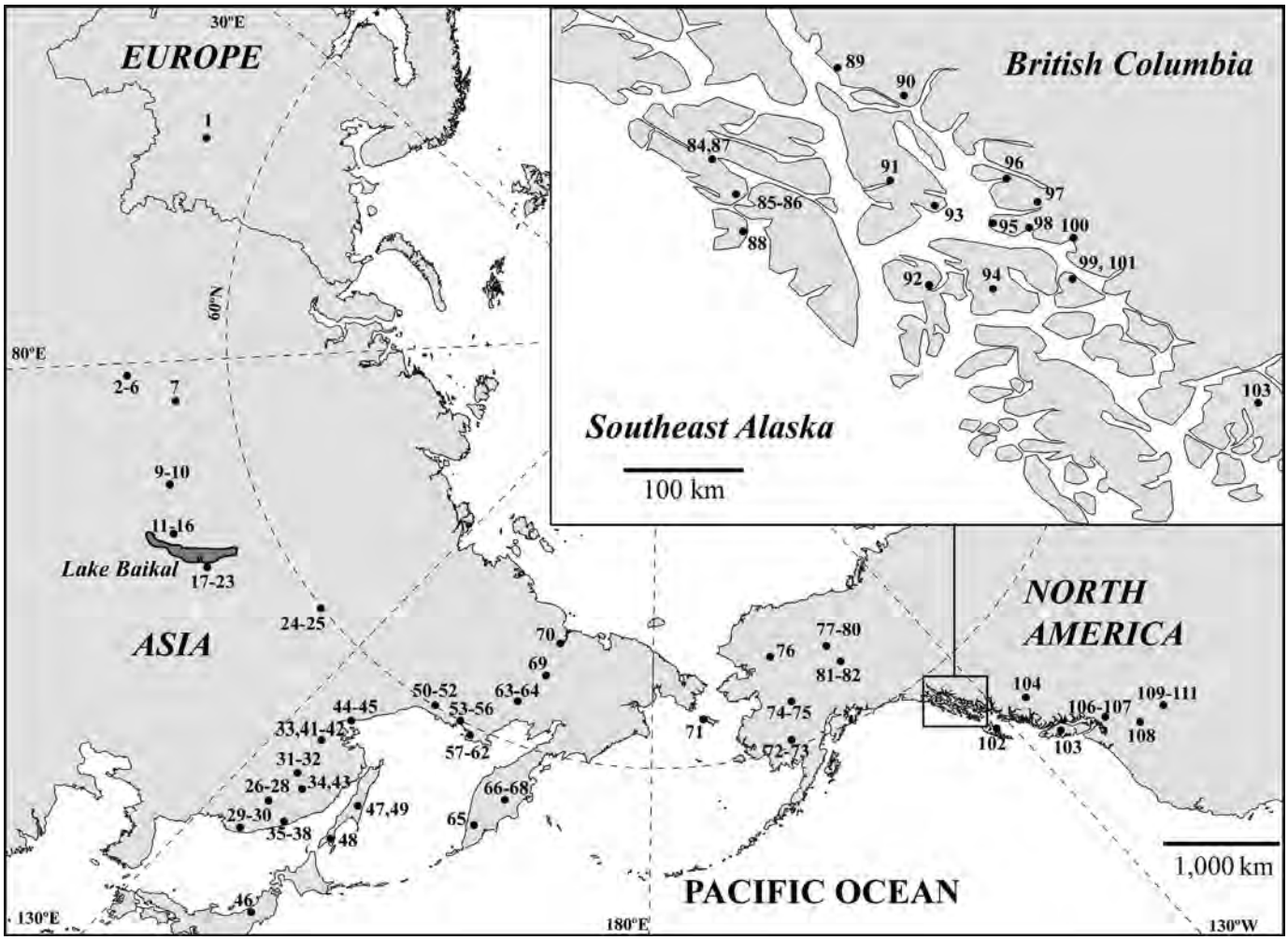

FIGURE 2. The distribution of *S. baturini* is based on published records and museum specimens and is centered on Beringia. Inset shows detail of localities in southeast Alaska. Numbers correspond to locality IDs in the Appendix.

worms with a commercial kit (AquaPure Genomic DNA Isolation Kit, Bio-Rad Laboratories, Hercules, California). A multilocus approach was employed to explore the potential for cryptic diversity in *S. baturini*. We assessed variation of 2 mitochondrial genes, nicotinamide dehydrogenase (ND4) and cytochrome oxidase I (COI). Phylogenetic species criteria (Adams, 1998; Brooks and McLennan, 2002; Nadler, 2002) were adopted in exploring whether *S. baturini* represents a single species among mustelids.

A 293–base pair (bp) region of the mitochondrial gene, COI (primers SoboCO1F 5′GCTCAGCTTCGGACAGTTTC3′ and SoboCO1R 5′TCATGCAAATGAACATCTAGGG3′; Tran [2003]) was used to test for reciprocal monophyly including 3 representatives of *S. baturini* from major geographic localities within its range (Table III). Outgroups were *Soboliphyme abei* (Asakawa et al., 1988) in *Sorex unguiculatus* Dobson from Japan and *Soboliphyme jamesoni* Read, 1952, in *Sorex tundrensis* Merriam from Yakutsk, Russia. An additional outgroup includes *Trichinella britovii* Pozio, La Rosa, Murrell, and Lichtenfels, 1992; *T. nativa* Britov and Boev, 1972; and *T. murelli* Pozio and LaRosa, 2000.

The ND4 gene was used to further resolve the intraspecific phylogenies as suggested by Blouin (2002). A 243-bp region of ND4 was amplified from 8 worms (Table II) by polymerase chain reaction (PCR) with primers SoboND4F 5′GGGAGGGCCACTTACCTTAT3′ and SoboND4R 5′GCCACAAACTTCTTCACGTCT3′. Primers for ND4 were designed with the use of Primer3 (Rozen and Skaletsky, 2000) on the basis of an alignment of published *Xiphinema americanum* Cobb, 1913 (GenBank NC005928), and *Trichinella spiralis* (Owen, 1835) (GenBank NC002681) ND4 genes.

Total reaction volumes were 25 μl consisting of 14.25 μl of H_2O; 1 μl of 10 μM primer each; 1 μl of DNA template (~5 ng/μl); 2.5 μl each of 25 mM $MgCl_2$, 10 mM DNTPs, and 10× PCR Buffer II; and 0.25 μl of Taq (5 units/μl, Amplitaq®, Applied Biosystems, Foster City, California). PCRs were run on PTC-200 thermocyclers (MJ Research, Waltham, Massachusetts) with the following parameters: initial denaturation at 94 C for 60 sec, subsequent denaturations for 30 sec, annealing at 67 C for 15 sec, and extension of 72 C for 30 sec, repeated for an additional 34 cycles, followed with a final extension of 72 C for 10 min. Product was visualized via electrophoresis on a 0.8% agarose gel and cleaned with 30% polyethylene glycol (PEG) and QiaQuick® cleanup kit (Qiagen Inc., Germantown, Maryland). BigDye® Terminator v.3.1 (Applied Biosystems) was used for cycle sequencing reactions. Excess dyes and primer were removed with Sephadex® G-50 spin columns or sodium acetate ethanol wash (Applied Biosystems). Forward and reverse strands were sequenced with an ABI PRISM® 3100 Genetic Analyzer.

Ambiguous sites were resolved with Sequencher™ 4.6 (Genecodes, Ann Arbor, Michigan). Alignments were made with ClustalW (Chenna et al., 2003). All sequences were identical in length and no insertions or deletions were necessary. Mitochondrial sequences were translated to amino acids and examined for stop codons to check against pseudogenes. Sequences were deposited in GenBank, and physical vouchers were deposited in the Museum of Southwestern Biology (Table II). In total, 8 adult and J_3 nematodes were sequenced from 6 mustelids and 2 soricids to examine the amount of sequence divergence among putative specimens of *S. baturini* (Table II).

TABLE I. Locality data for mustelids that were examined for *S. baturini* throughout northwest North America. Prevalences and mean intensities of *S. baturini* from each locality are indicated.

Scientific name	n	Prevalence	Mean intensity	Range	Locality	State/Province	Latitude	Longitude
Gulo gulo	1	0	0	0	Yukon Flats	Alaska	66.15	−147.55
Martes americana	10	0	0	0	100-Mile House	British Columbia, Canada	51.71	−121.55
M. americana	10	0	0	0	Enderby	British Columbia, Canada	50.68	−119.05
M. americana	22	4.5	1	1	Francois Lake	British Columbia, Canada	53.98	−126.43
M. americana	57	0	0	0	Kootenai National Park	British Columbia, Canada	50.47	−115.67
M. americana	14	78.6	14.7	1–38 ± 12.2	Kuiu Island	Alaska	56.72	−133.92
M. americana	75	85.3	20.7	1–200 ± 29.8	Kupreanof Island	Alaska	56.79	−133.50
M. americana	17	94.1	27.3	10–53 ± 15.2	Mitkof Island	Alaska	56.68	−132.92
M. americana	45	0	0	0	Norman Wells	Northwest Territories, Canada	65.23	−127.00
M. americana	5	0	0	0	Prince George	British Columbia, Canada	54.44	−123.39
M. americana	9	22.2	5.5	2–9 ± 4.9	Revillagigedo Island	Alaska	55.77	−131.60
M. americana	10	0	0	0	Smithers	British Columbia, Canada	54.75	−126.65
M. americana	133	53.4	12	1–80 ± 15.9	Thomas Bay	Alaska	57.02	−132.85
M. americana	41	2.4	1	1	Yukon Flats	Alaska	66.15	−147.55
M. caurina	56	87.5	21.9	3–97 ± 16.9	Admiralty Island	Alaska	57.20	−134.29
M. caurina	5	0	0	0	Idaho	Idaho	44.96	−113.64
M. caurina	3	0	0	0	Montana	Montana	48.20	−114.30
M. caurina	58	1.7	1	1	Vancouver Island	British Columbia, Canada	49.17	−123.93
M. pennanti	59	0	0	0	Central BC	British Columbia, Canada	52.00	−123.67
Mustela erminea	10	0	0	0	100-Mile House	British Columbia, Canada	51.71	−121.55
M. erminea	2	50	1	1	Admiralty Island	Alaska	57.20	−134.29
M. erminea	10	0	0	0	Fort Nelson	British Columbia, Canada	58.83	−123.75
M. erminea	10	0	0	0	Kupreanof Island	Alaska	56.79	−133.50
M. erminea	11	0	0	0	Mitkof Island	Alaska	56.68	−132.92
M. erminea	1	0	0	0	Queen Charlotte Islands	British Columbia, Canada	53.25	−132.00
M. erminea	7	0	0	0	Smithers	British Columbia, Canada	54.75	−126.65
M. erminea	5	0	0	0	Thomas Bay	Alaska	57.02	−132.85
M. erminea	7	0	0	0	Vancouver Island	British Columbia, Canada	49.17	−123.93
Neovison vison	1	0	0	0	100-Mile House	British Columbia, Canada	51.71	−121.55
N. vison	5	0	0	0	Enderby	British Columbia, Canada	50.68	−119.05
N. vison	5	0	0	0	Francois Lake	British Columbia, Canada	53.98	−126.43
N. vison	1	0	0	0	Kupreanof Island	Alaska	56.79	−133.50
N. vison	1	100	1	1	Mitkof Island	Alaska	56.68	−132.92
N. vison	2	0	0	0	Montana	Montana	48.20	−114.30
N. vison	7	0	0	0	Prince George	British Columbia, Canada	54.44	−123.39
N. vison	1	0	0	0	Smithers	British Columbia, Canada	54.75	−126.65
N. vison	2	0	0	0	Vancouver Island	British Columbia, Canada	49.17	−123.93
Taxidea taxus	2	0	0	0	Washington	Washington	47.00	−120.00

TABLE II. Specimens of *S. baturini* used in constructing the haplotype network for ND4 sequences. Specimens were obtained through the Beringian Coevolution Project or other collaborators throughout the Beringian region. Museum of Southwestern Biology and GenBank accession numbers, host species, host status (definitive or paratenic), and locality data are included.

Specimen	GenBank	Host species	Host style	Country	Locality	Latitude	Longitude
NK 135687	EF457895	*Martes americana*	Definitive	U.S.	Kupreanof Island	56.73	−133.57
NK 128108	EF457893	*M. americana*	Definitive	U.S.	Fairbanks, Alaska	65.18	−146.58
NK 122046	EF457892	*M. caurina*	Definitive	U.S.	Admiralty Island	57.28	−134.03
NK 159571	EF457891	*M. zibellina*	Definitive	Russia	Kamchatka	56.00	160.00
NK 122064	EF457890	*Mustela erminea*	Definitive	U.S.	Admiralty Island	57.44	−133.84
NK 122289	EF457896	*Neovison vison*	Definitive	U.S.	Mitkof Island	56.68	−132.92
NK 159582	EF457894	*Sorex cinereus*	Paratenic	U.S.	Eagle, Alaska	63.83	−142.16
NK 159576	EF457889	*S. unguiculatus*	Paratenic	Russia	Lazovski	43.28	134.05

TABLE III. Specimens of *Soboliphyme* used in constructing the MrBayes tree for COI sequences. Specimens were obtained through the Beringian Coevolution Project or other collaborators throughout the Beringian region. Museum of Southwestern Biology and GenBank accession numbers, host species, and locality data are included.

Specimen	GenBank	Species	Host species	Country	Locality	Latitude	Longitude
NK 135687	EF519531	*Soboliphyme baturini*	*Martes americana*	U.S.	Kupreanof Island	56.73	−133.57
NK 128108	EF519532	*S. baturini*	*M. americana*	U.S.	Fairbanks, Alaska	65.18	−146.58
NK 159571	EF519530	*S. baturini*	*M. zibellina*	Russia	Kamchatka	56.00	160.00
NK 139168	EF519533	*S. jamesoni*	*Sorex tundrensis*	Russia	Yakutsk	62.02	129.61
NK 139584	EF519534	*S. jamesoni*	*S. roboratus*	Russia	Yakutsk	62.07	128.94
NK 159581	EF519535	*S. abei*	*S. unguiculatus*	Japan	Hokkaido	43.05	141.35
NA	DQ007892	*Trichinella britovi*	NA	NA	NA	NA	NA
NA	DQ007894	*T. murrelli*	NA	NA	NA	NA	NA
NA	AB252966	*T. nativa*	NA	NA	NA	NA	NA

Maximum parsimony (MP) optimality criteria was used for phylogenetic reconstruction by PAUP* (Swofford, 2002), considering all characters as unordered with 4 possible states (A, C, G, T); uninformative characters were excluded from the MP analysis. A branch and bound search was performed with COI sequences. Node support was evaluated with nonparametric bootstrap methodology and the use of 5,000 replicates for MP (Felsenstein, 1985). The Markov chain Monte Carlo (MCMC) sampling procedure was performed by the program MrBayes (Ronquist and Huelsenbeck, 2003) to estimate the posterior probability of phylogenetic trees. The program was executed twice with 5,000,000 generations run, 4 heated chains, and 45,000 trees saved. The median joining algorithm (Bandelt et al., 1999) in the program Network v4.1.1.2 (Fluxus Engineering, Suffolk, U.K.) was used to create a haplotype network for the 8 sequences of the ND4 gene (Table II).

RESULTS

Host surveys

Examination of historical accounts of *S. baturini*, along with data from the current study (Appendix), indicate that *S. baturini* is found predominantly in *M. americana*, *M. caurina*, and *M. zibellina*. Of 756 mustelids necropsied, 204 (27%) were infected and 3,674 specimens of *S. baturini* were recovered (Fig. 1; Table I). No *S. baturini* were found in *G. gulo* (n = 1), *M. pennanti* (n = 59), or *T. taxus* (n = 2). Only 1 *M. erminea* (n = 70) and 1 *N. vison* (n = 40) were infected, both in southeast Alaska. The highest prevalence of *S. baturini* in *M. americana* was from southeast Alaska. Of those hosts surveyed near the eastern boundary of the known range for *S. baturini*, only 1 worm was found (Francois Lake, interior British Columbia, n = 114) and none was found in the Northwest Territories (n = 45). *Martes caurina* had the highest prevalence of infection on Admiralty Island (88%) and *M. americana* had highest prevalences on Kuiu (79%), Kupreanof (85%), and Mitkof islands (94%).

Assessment of distribution from current and historical data

Records of occurrence of *S. baturini* in North America, including those from this study, were mapped over the current distribution of the principle hosts, *M. americana* and *M. caurina* (Fig. 1). Two equivocal historical records of *S. baturini* occurred farther east in North America. A specimen of *S. baturini* reported from Madison, Wisconsin (Morgan, 1943), is unsubstantiated because the author does not refer to any specific locality. This specimen was identified at the USNPC by B. Chitwood in 1933, where the practice used at that time often referred geographic records to the city or laboratory, rather than to the actual geographic origin of the specimen. Another account of *S. baturini* was recovered in a single wolverine (*G. gulo*) from the province of Quebec, Canada (Bezdek, 1942). Because wolverines are long-distance dispersers (Hornocker and Hash, 1981) and infections of *S. baturini* can persist for 20 mo (Karmanova, 1986), this record might have been a chance dispersal event. Alternatively, that specimen could have been sent to a laboratory in Quebec from a western locality. If these 2 records are discounted, then the eastern limit of viable *S. baturini* populations would be the Rocky Mountains. We suggest this to be the case on the basis of the ease of detection of this large stomach-dwelling nematode combined with a series of published assessments of diets of mustelids in North America. In addition, extensive parasitological surveys of mustelids and other potential carnivore hosts east of the Rocky Mountains have not detected this parasite (Erickson, 1946; Meyer and Chitwood, 1951; Dick and Leonard, 1979; Jennings and Threlfall, 1982; Poole et al., 1983).

The Old World distribution of *S. baturini* appears limited to the region east of the Ural Mountains. Accounts of *S. baturini* west of the Urals may be attributed to human translocations of *M. zibellina* from the Baikal region after their earlier extirpation (Monakhov, 2001).

Molecular identification of nematodes

Molecular analysis does not refute the hypothesis that *S. baturini* is a single widespread species. Sequences of COI from 3 putative adult *S. baturini* representing populations from disparate geographic localities in the Nearctic and Palearctic exhibited minimal variation, and MP analyses unequivocally demonstrated reciprocal monophyly relative to the presumptive sister species *S. abei* and *S. jamesoni* (Fig. 3). After initial assessment of this locus aimed at species-level identification, our focus shifted from COI to ND4 on the basis of expectations of greater variability and information content to explore variation in worms from different hosts at particular sites.

Sequences at the ND4 locus could not be reliably aligned between *S. baturini* and respective outgroups. Minimal diversity was demonstrated in sequences of ND4 for 6 adults and 2 J_3 larvae. Nematodes found in different mustelid hosts collected from similar geographic locations had identical sequences for

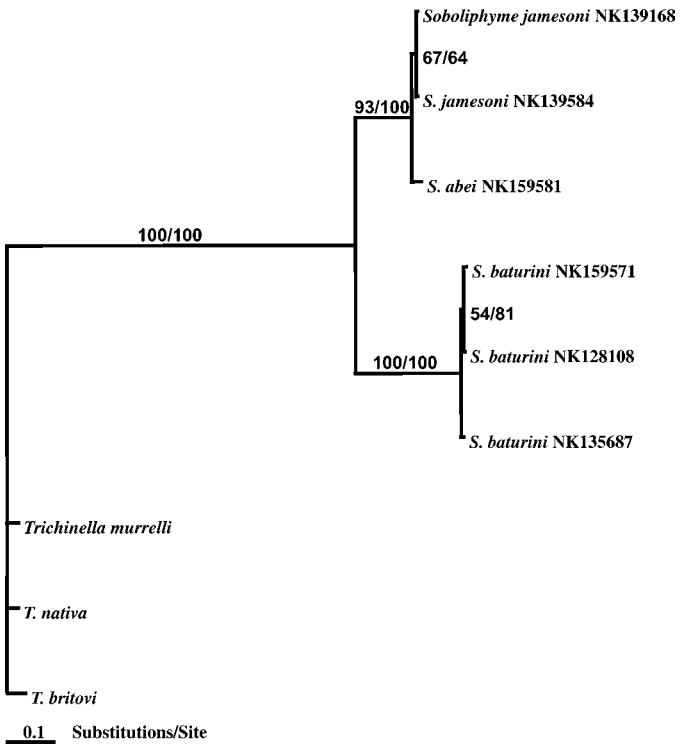

FIGURE 3. Reciprocal monophyly is established for *S. baturini* with a majority consensus tree for maximum parsimony. A maximum parsimony tree was generated with an exhaustive search from 293 bp of the COI mtDNA gene sequences of *S. baturini*, *S. abei*, *S. jamesoni*, and *Trichinella* sp. MrBayes tree topology has both Bayesian and MP nodal supports listed (Bayesian/MP). Trees were rooted with *Trichinella* sp. Major and minor subdivisions are illustrated.

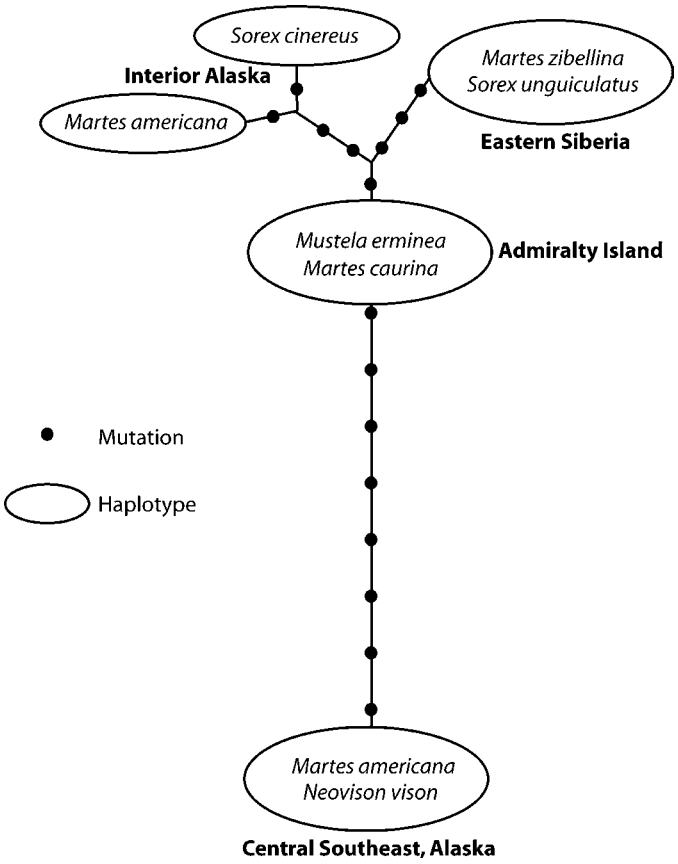

FIGURE 4. Network of *S. baturini* haplotypes (243 bp of the ND4 gene) constructed by the median joining method. Juvenile *S. baturini* (soricid hosts) are similar to adult *S. baturini* (mustelid hosts). Nematodes of *Neovison vison* and *M. erminea* are identical to nematodes in *M. caurina* and *M. americana*. Dots represent mutational changes. Ovals indicate haplotypes.

central southeast Alaska (*M. americana*, *N. vison*) and Admiralty Island (*M. caurina*, *M. erminea*), respectively (Fig. 4). Sequences of specimens from putative *S. baturini* in soricids from Russia and Alaska also were identical or differed minimally when compared with worms inhabiting mustelids from the same geographic regions (Fig. 4). For example, nematode sequences from *M. zibellina* and *S. unguiculatus* Dobson were identical and differed by only 2 bp between *M. americana* and *S. cinereus* Kerr collected from 2 localities separated by 300 km in interior Alaska. This is evidence that shrews are paratenic hosts and that at any particular locality these worms are infecting a variety of hosts. Additionally, diet of New World marten and Old World sable (Table IV) indicated that shrews are consumed frequently.

DISCUSSION

Sampling

Identifying the role of putative hosts in a parasite's life cycle (e.g., definitive, intermediate, or paratenic) is essential to understanding the evolutionary history and assessing the significance of processes such as ecological fitting in host/parasite dynamics. Wide taxon and geographic sampling is required to first document the range of a parasite, identify species limits, and characterize the role of component hosts. Here, we establish species identity, describe the geographic range, and identify the paratenic and definitive host associations of the Holarctic nematode, *S. baturini*.

Genetic diversity and species

Minimal genetic diversity was observed in putative populations of *S. baturini* (Fig. 3; Table III). Application of phylogenetic criteria (e.g., Adams, 1998; Brooks and McLennan, 2002; Nadler, 2002) establishes *S. baturini* as a single species. Cryptic species and species complexes have been reported and predicted among assemblages of Beringian helminths, including nematodes and cestodes (Hoberg et al., 1999; Haukisalmi, 2001, 2004) as a consequence of the complex history of faunal expansion and geographic colonization and isolation in this region. Among a diversity of parasitic helminths, minimal variation in morphological characters contrasts with ''hidden molecular diversity,'' a general phenomenon for helminths in Beringia and elsewhere (Hoberg et al., 2003; Haukisalmi et al., 2004; Cook et al., 2005). *Soboliphyme baturini* might be an exception to this generality (Koehler, 2006). Molecular comparisons did not detect substantial genetic variation among nematodes from different hosts, a finding consistent with the hypothesis that *S. baturini* represents a single species across its wide geographic range that spans Beringia (Koehler, 2006).

Low genetic diversity, multiple hosts, and relatively widespread geographic distribution suggest a shallow temporal association for *S. baturini* and mustelids that could be compatible with a history of geological and host colonization. Molecular characterization of *S. baturini* occurring in *G. gulo* and *M. pennanti* is still needed.

Geographic range and life cycle

The distribution of *S. baturini* in marten from 3 major localities throughout Alaska was mapped (Zarnke et al., 2004; Fig. 1) on the basis of the following prevalences: northern (19%, n = 2,166), southwestern (30%, n = 1,058), and southeastern (47%, n = 3,028). Our expanded survey of marten and other mustelid hosts demonstrated high prevalences in southeast Alaska (64% n = 334). Only 1 worm was found east of the Coast Range (Table I; Fig. 1), suggesting that the distribution of *S. baturini* is restricted primarily to the Pacific Northwest.

The absence of *S. baturini* in central and eastern North America can be attributed to the distribution of intermediate hosts required for transmission. Experimental evidence found that only oligochaetes from the Enchytraeidae were suitable hosts for development of *S. baturini* (Karmanova, 1963). Enchytraeids are found on every continent, with greatest abundance in moist temperate regions (O'Connor, 1967). Karmanova (1986) concluded that the distribution of *S. baturini* was dependant on geography and meteorological conditions and potentially limited by availability of suitable enchytraeids. She found *S. baturini* most common in floodplains of major rivers in eastern Asia where enchytraeids thrive in areas of humid forest litter. During periods of drought, enchytraeids survive near water sources but perish during periods of extended flooding. Kaufmann et al. (2002) showed that enchytraeids colonize soils within 40 yr of deglaciation, so their distribution would be limited by rates of geographic expansion as glaciers retreat. Consequently, the temperate rainforest climate of southeast Alaska and associated refugial habitats appear to have been ideal for the persistence of *S. baturini* during full glacial advances of the Late Pleistocene (Koehler, 2006). Future identification of specific enchytraeids capable of hosting *S. baturini*, and then careful documentation of the distributions of these hosts, could substantially broaden our understanding of the geographic limits of this nematode.

Among the vast array of definitive hosts examined (Appendix), only a few are thought to be important to the life cycle of *S. baturini*. Reviews by Kontrimavichus (1985) and Karmanova (1986) concluded that marten and sable were the principle definitive hosts. In North America, coastal Alaska and British Columbia have a high prevalence of *S. baturini* in both *M. caurina* and *M. americana* (59%, n = 362), whereas other mustelids (i.e., *N. vison* [25%, n = 4] and *M. erminea* [3%, n = 36]) had lower prevalence, although sample size is low for both. If *N. vison* and *M. erminea* were essential to the life cycle of *S. baturini*, one might expect higher prevalence and the parasite should be common in those hosts when marten are not in sympatry.

Kontrimavichus (1962) examined 707 mustelids from the Khabarovsk region of the Russian Far East, including 281 *N. vison* (91% infected), 196 *M. sibirica* Pallas (39% infected), and 196 *M. zibellina* (70% infected). The author noted that *N. vison* might be more susceptible to infection because of close association with water. Larger samples of *N. vison* are needed in North America to effectively understand the role of this host in the Pacific Northwest.

Sporadic cases of *S. baturini* in *G. gulo* have been reported from Montana (Price, 1930), Quebec (Bezdek, 1942), and interior Alaska (USNPC 033728). Rausch (1959) examined 108 *G. gulo* from throughout northern and interior Alaska and reported no *S. baturini*. When found in *G. gulo*, specimens have been mature adults. The Holarctic distribution (Wilson and Reeder, 2005) and large dispersal capabilities for wolverines (Hornocker and Hash, 1981) suggest they may have been crucial to the dissemination and maintenance of *S. baturini* throughout its geographic range. Another mustelid, *M. pennanti*, has been recorded as a host to *S. baturini* in Montana (USNPC 067206) and in southeast Alaska (AF 24441). The absence of *S. baturini* in 59 *M. pennanti* collected from throughout British Columbia and 162 *M. pennanti* from Manitoba (Dick and Leonard, 1979) reinforces the conclusion that *M. pennanti* is an uncommon host for *S. baturini*. Populations of *M. pennanti* in Washington, Oregon, and Montana should be screened for *S. baturini*. The appearance of *S. baturini* in *M. pennanti* could be the result of ecological fitting (Janzen, 1985; Brooks et al., 2006), where parasites track a resource provided by the host, rather than as a manifestation of the host specificity. Ecological fitting could be applied to other hosts (e.g., *N. vison* and *M. erminea*) as well because deep coevolutionary, or even cophylogeographic relationships, have not been demonstrated (Koehler, 2006). A temporally shallow association is consistent with minimal genetic diversity relative to hosts and geography.

When the situation arises, *S. baturini* can infect other species because resources required to complete its life cycle are available. In addition to the potential role of refugia (e.g., coastal and Beringia) in the evolution of this nematode (Fleming and Cook, 2002; Cook et al., 2006), resources available to *S. baturini* in marten apparently are optimal along the coast and in interior Alaska. Zarnke et al. (2004) arrived at a similar conclusion, suggesting that some environmental condition in southeast Alaska favors the survival and transmission of *S. baturini*.

Absence of *S. baturini* from European marten (*Martes martes* (Linnaeus) or *Martes foina* (Erxleben)) could result from constraints of historical biogeography (*S. baturini* never occurred in Europe), diet (paratenic or intermediate hosts), or features of the hosts related to this nematode's ability to track resources available only in *M. americana*, *M. caurina*, and *M. zibellina*. For comparison with another nematode, *M. martes* and *M. foina* are hosts to *Skrjabingylus petrowi* Bageanov, 1936. This nematode of the frontal sinuses does not occur naturally in *M. zibellina* or North American marten (Kontrimavichus, 1985; Kontrimavichus et al., 1985; Koubek et al., 2004). As with *S. baturini*, soricids have been implicated as paratenic hosts for species of *Skrjabingylus* (Gamble and Riewe, 1982). Hence, diet does not appear to be a limiting factor in the contrasting distributions of these 2 nematodes because soricids are eaten by *M. foina* and *M. martes* (Clevenger, 1994; Helldin, 1999).

Soboliphyme baturini might fail to achieve sexual maturity in *M. erminea*. Schmidt and Kinsella (1965) reported juvenile *S. baturini* in *M. erminea* collected near Juneau, Alaska. *Mustela erminea* from our study were infected only by juvenile *S. baturini*. Additional specimens of this nematode recovered from

TABLE IV. Summary of diet analyses of *Martes* spp. used to determine whether shrews are important to the diet of *Martes* spp. Studies are from a range of localities throughout the Palearctic and Nearctic distribution of *Martes* spp. Studies examined stomach contents unless otherwise noted. The amount of vegetation and soil debris in the diet is also reported.

Locality	Species	n	Shrew prevalence (%)	Debris	Source
Algonquin Park, Ontario, Canada	*Martes americana*	118	13.0	Debris	Francis and Stephenson, 1972
Ontario, Canada	*M. americana*	392	13.0	No mention	Thompson and Colgan, 1987
Western Newfoundland, Canada	*M. americana*	56	10.7	No mention	Bateman, 1968
Newfoundland, Canada	*M. americana*	704	9.9	No mention	Gosse and Hearn, 2005
Glacier National Park, Montana	*M. americana*	1,758	7.6	No mention	Weckwerth and Hawley, 1962
Northern British Columbia, Canada	*M. americana*	127	7.5	No mention	Quick, 1955
Maine	*M. americana*	412	7.0	No mention	Soutiere, 1979
Sequoia National Forest, California	*M. caurina*	150 scat	6.7	Woody debris 23%, rock 2%	Zielinski and Duncan, 2004
Alberta and British Columbia, Canada	*M. americana*	112	3.5	Moss 1%	Cowan and Mackay, 1950
Southeast Manitoba, Canada	*M. americana*	107	1.9	Vegetation 12%	Raine, 1987
South-central Alaska	*M. americana*	467	1.7	Inorganic matter ignored	Buskirk and MacDonald, 1984
Northwest Territories, Canada	*M. americana*	172	1.2	58% debris	Douglass et al., 1983
Selway Bitterroot Wilderness, Montana	*M. americana*	129	1.0	No mention	Koehler and Hornocker, 1977
Grand Teton National Park, Wyoming	*M. americana*	528	0.7	Mentions specific berries only	Murie, 1961
Interior Alaska	*M. americana*	466	0	No mention	Lensink et al., 1955
Northwestern Montana	*M. americana*	64	0	Lichen and grass	Marshall, 1946
Colorado	*M. caurina*	32	45.0	17% vegetation	Gordon, 1986
Yosemite National Park, California	*M. caurina*	40	8.0	Debris and vegetation 63%	Hargis and McCullough, 1984
Northeast Oregon	*M. caurina*	1,014	6.4	5% wood, lichen, grass	Bull, 2000
Tahoe National Forest, California	*M. caurina*	300 scat	2.2	Vegetation 8%	Zielinski et al., 1983
Vancouver Island, British Columbia, Canada	*M. caurina*	701	1.6	45% conifer needles, moss, fern fronds	Nagorsen et al., 1989
Queen Charlotte Islands, British Columbia, Canada	*M. caurina*	97	0	74% vegetation	Nagorsen et al., 1991
Scotland	*M. martes*	174	0	Debris	Putman, 2000
Shantar Islands, Russia	*M. zibellina*	152	2.0	No mention	Dulkeit, 1929
Northern China	*M. zibellina*	221	0	No mention	Buskirk et al., 1996
Magadan region, Kava River, Russia	*M. zibellina*	30	10.0	Seeds 50%, berry 3%	Ivanov, 1985
Magadan region, Kava River, Russia	*M. zibellina*	14	46.1	Seeds 23%, berry 14%	Ivanov, 1985
Magadan region, Bolshoi Anyui River, Russia	*M. zibellina*	79	2.5	Seeds 25%	Ivanov, 1985
Magadan region, Chelomdzha River, Russia	*M. zibellina*	30	6.7	Seeds 63%, berries 3–10%, fruits 60%	Ivanov, 1985
Magadanski preserve, Russia	*M. zibellina*	1,552	3.9	Seeds 16%, berries and fruits 25%	Devyatkin and Ivanov, 1995

M. erminea are needed to fully explore this contention. Scarcity of *S. baturini* in *M. erminea* might also be attributed to the relatively large size of the nematode, a factor that might inhibit its occurrence in the stomach of smaller mustelids. Constraints of host and parasite body size are reviewed in Poulin (1998). Therefore, ermine could be considered an incidental host and subsequently might not be significant in shaping the evolutionary past of *S. baturini*.

Paratenic hosts, diet, and transmission

Experimental infections by ingestion found that only oligochaetes from the Enchytraeidae were suitable intermediate hosts for *S. baturini* (Karmanova, 1963). Whether the definitive host directly consumes the infected enchytraeid or is first eaten by a paratenic host has been debated (Domnich, 1982; Karpenko, 1985; Kontrimavichus, 1985; Karmanova, 1986; Karpenko et

al., 1998, 2007; Dokuchaev, 2003; Zarnke et al., 2004). Domnich (1982) proposed that shrews serve as paratenic hosts on the basis of morphological similarities between adult *S. baturini* in mustelids and encysted juvenile nematodes in the diaphragms of shrews. Dokuchaev (2001, 2003) concluded that the high prevalence of juvenile *S. baturini* (up to 50) in soricids was a sufficient year-round source for the maintenance of infection in mustelids.

Molecular evidence revealed that J_3 nematodes in shrews were identical to definitively identified adult *S. baturini* in mustelids (Fig. 4) from the same localities, thus lending support to the hypothesis that a paratenic relationship exists. Recovery of mature *S. baturini* from a mustelid that was fed juvenile nematodes from infected shrews would unequivocally demonstrate a role in transmission for species of *Sorex* and perhaps other soricomorphs.

Juvenile *S. baturini* found in the diaphragms of shrews should not be confused with adults representing 8 other species of *Soboliphyme* known to reach sexual maturity in the stomachs of soricomorphs (*S. abei*, Asakawa et al., 1988; *S. ataahai* Ganzoring et al., 2002; *S. caucassica* Matsaberidze, 1965; *S. hirudiniformis* Kirshenblat, 1964; *S. jamesoni* Read, 1952; *S. occidentalis* Ribas and Casanova, 2004; *S. soricis* Baylis and King, 1932; *S. urotrichi* Machida and Uchida, 1982). Karpenko et al. (2007) reported finding juvenile *S. baturini* in species of *Sorex* from Asia and for the first time from North America. Juvenile *S. baturini* have also been reported in *Myodes rufocanus* (Sundevall) (Karpenko et al., 1998), but their identity has not been confirmed with molecular genetic assessment.

Existing literature on diets of *M. americana* and *M. caurina* indicates that these mustelids eat shrews (Table IV). Of the 27 papers examined on marten diet, 81% reported shrews in the diet. Shrews composed 8.8% of the diet on average, with a range of 0.7% to 46%. Gordon (1986) reported that 45% of the diet in a population of Colorado marten consisted of shrews. She hypothesized that marten consumed shrews during severe winters when the typical prey base was unavailable. An alternative hypothesis regarding mustelid infections of *S. baturini* would be the ingestion of oligochaetes, either accidentally with debris on food items or by direct consumption. About 50% of the diet literature examined mentioned plant or soil debris in the host digestive tracts (Table IV); thus, the exact mechanism for infection could involve multiple pathways.

Molecular evidence now links the juveniles of *S. baturini* in shrews with mature *S. baturini* in definitive mustelid hosts at the same geographic locations. Shrew consumption by marten also has been thoroughly documented. What remains unresolved is the extent to which marten hosts become infected with *S. baturini* as a result of consuming infected shrews. Soricomorphs are distributed throughout a variety of habitats (Nagorsen et al., 1996) and are frequently sympatric with mustelids. The abundance of shrews, and prevalence of infection for *S. baturini* in potential paratenic hosts, might serve as key determinants of the distribution of this nematode among mustelids across high-latitude environments. In turn, the use of parasitic juvenile and egg stages greatly increases the availability and scope of material to phylogeneticists and population geneticists, who often lack sufficient samples from remote or politically inaccessible localities (e.g., Jenkins et al., 2005).

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APPENDIX. Summary of reported carnivore, rodent, and soricomorph hosts of *S. baturini* from throughout its Holarctic distribution. Role in the life cycle is indicated for both definitive and paratenic hosts. Host ID numbers correspond to the specimens in Figure 2. Locality data, including specific locality, country, and approximate latitude and longitude, are also included. Data from unpublished collections: AF = University of Alaska Museum; AK = Alaska; BC = British Columbia; Is. = Island; NWR = National Wildlife Refuge; USNPC = U.S. National Parasite Collection; WA = Washington.

Host	Common name	Role	ID	Locality	Country	Author/Data source	Latitude	Longitude
Alopex lagopus	Arctic fox	D	71	St. Lawrence Is., AK	U.S.	Rausch et al., 1990	63.70	−171.70
Felis catus	Domestic cat	D	66	Kamchatka	Russia	Petrov, 1930	56.00	160.00
Gulo gulo	Wolverine	D	80	Brooks Range, AK	U.S.	Swanson, USNPC 084031.00	68.00	−147.00
G. gulo	Wolverine	D	20	Buryatia, east of Lake Baikal	Russia	Kontrimavichus, 1985	53.00	109.00
G. gulo	Wolverine	D	111	Montana	U.S.	Price, 1930	46.58	−112.03
G. gulo	Wolverine	D	112	Quebec	Canada	Bezdek, 1942	54.00	−72.00
G. gulo	Wolverine	D	17	Russia, Baikal	Russia	Kontrimavichus, 1985	53.00	107.67
Lutra lutra	European otter	D	2	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
Martes americana	American marten	D	77	Chena River, Fairbanks	U.S.	Swartz, 1968; this study	64.83	−147.70
M. americana	American marten	D	84	Chichagof Is., AK	U.S.	This study	57.87	−135.77
M. americana	American marten	D	98	Farragut Bay, AK	U.S.	This study	57.12	−133.23
M. americana	American marten	D	104	Francois Lake, BC	Canada	This study	53.98	−126.43
M. americana	American marten	D	94	Kupreanof Is., AK	U.S.	This study	56.78	−133.48
M. americana	American marten	D	74	McGrath, AK	U.S.	This study	63.13	−156.52
M. americana	American marten	D	101	Mitkof Is., AK	U.S.	This study; Bezdek, 1942	56.58	−132.80
M. americana	American marten	D	76	Northern Alaska	U.S.	Zarnke et al., 2004	70.00	−151.50
M. americana	American marten	D	97	Port Houghton, AK	U.S.	This study	57.32	−133.33
M. americana	American marten	D	95	Pt. Highland, AK	U.S.	This study	57.15	−133.45
M. americana	American marten	D	103	Revillagigedo Is., AK	U.S.	This study	55.65	−131.50
M. americana	American marten	D	87	Southeastern Alaska	U.S.	Zarnke et al., 2004	57.80	−135.70
M. americana	American marten	D	75	Southwestern Alaska	U.S.	Zarnke et al., 2004	62.96	−155.60
M. americana	American marten	D	100	Thomas Bay, AK	U.S.	This study	57.02	−132.85
M. americana	American marten	D	96	Windham Bay, AK	U.S.	This study	57.57	−133.45
M. americana	American marten	D	106	Wisconsin, Madison	U.S.	Morgan, USNPC 044742.00	48.45	−121.10
M. americana	American marten	D	79	Yukon Flats, AK	U.S.	This study	66.15	−147.55
M. americana	American marten	D	88	Kruzof Is., AK	U.S.	AF 19914	57.13	−135.55
M. caurina	American marten	D	91	Admiralty Is., AK	U.S.	This study	57.53	−134.25
M. caurina	American marten	D	109	Idaho	U.S.	Marshall, USNPC 043903.02	45.00	−115.00
M. caurina	American marten	D	92	Kuiu Is., AK	U.S.	This study	56.53	−134.05
M. caurina	American marten	D	102	Queen Charlotte Islands, BC	Canada	This study	53.25	−132.00
M. caurina	American marten	D	105	Vancouver Island, BC	Canada	This study	49.67	−125.83
M. caurina	American marten	D	107	Washington (North Cascades)	U.S.	Hoberg et al., 1990	47.00	−120.00
M. caurina	American marten	D	108	Pullman, WA	U.S.	Gorham, USNPC 047327.00	46.72	−117.17
M. flavigula	Yellow-throated marten	D	43	Khabarovskii krai	Russia	Kontrimavichus, 1985	48.01	136.81
M. flavigula	Yellow-throated marten	D	26	Primorskii krai	Russia	Kontrimavichus, 1985	46.00	134.00
M. melampus	Japanese marten	D	46	Akita, Aomori	Japan	Sato et al., 1999	39.75	140.08
M. pennanti	Fisher	D	110	Montana, Flathead	U.S.	Worley, USNPC 067206.00	47.88	−114.12
M. pennanti	Fisher	D	89	Juneau, AK	U.S.	AF 24441	58.58	−134.83
M. zibellina	Sable	D	3	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
M. zibellina	Sable	D	11	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
M. zibellina	Sable	D	67	Kamchatka	Russia	Kontrimavichus, 1985	56.00	160.00
M. zibellina	Sable	D	41	Khabarovskii krai	Russia	Kontrimavichus, 1985	51.20	136.74
M. zibellina	Sable	D	10	Tuva	Russia	Kontrimavichus, 1985	53.00	96.00
M. zibellina	Sable	D	53	Chelomdzha River, Magadan	Russia	Domnich and Obushenkov, 1983	60.27	147.61
M. z. kamtschadalica	Sable	D	68	Kamchatka	Russia	Kontrimavichus, 1985	56.00	160.00

APPENDIX. Continued.

Host	Common name	Role	ID	Locality	Country	Author/Data source	Latitude	Longitude
M. z. princeps	Sable	D	18	Trans Baikal region	Russia	Kontrimavichus, 1985	53.00	107.67
M. z. sahalinensis	Sable	D	49	Sakhalin Is.	Russia	Shimakura and Odajima, 1934	51.00	143.00
Meles meles	European badger	D	4	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
Mustela altaica	Mountain weasel	D	21	Buryatia, east of Lake Baikal	Russia	Kontrimavichus, 1985	53.00	109.00
M. altaica	Mountain weasel	D	12	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
M. erminea kaneii	Baikal ermine	D	13	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
M. erminea	Ermine	D	93	Admiralty Island, AK	U.S.	Koehler, unpubl. data	57.44	−133.84
M. erminea	Ermine	D	69	Omolon R., Chukotka	Russia	Domnich and Obushenkov, 1983	65.23	160.55
M. erminea	Ermine	D	90	Juneau, AK	U.S.	Schmidt and Kinsella, 1965	58.40	−134.50
M. erminea	Ermine	D	8	Tuva	Russia	Kontrimavichus, 1985	51.50	95.00
M. erminea	Ermine	D	24	Yakutia	Russia	Kontrimavichus, 1985	60.00	121.00
M. erminea	Ermine	D	70	Lower Kolyma River, Yakutia	Russia	Gubanov, 1964	68.54	160.82
M. eversmanni	Steppe polecat	D	22	Buryatia, east of Lake Baikal	Russia	Kontrimavichus, 1985	53.00	109.00
M. e. michnoi	Baikal steppe polecat	D	14	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
M. lutreola	European mink	D	1	Chuvashia	Russia	Kontrimavichus, 1985	55.50	47.00
M. nivalis	Least weasel	D	39	Khabarovskii krai	Russia	Kontrimavichus, 1985	49.31	136.53
M. sibirica	Siberian weasel	D	5	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
M. sibirica	Siberian weasel	D	23	Buryatia, east of Lake Baikal	Russia	Kontrimavichus, 1985	53.00	109.00
M. sibirica	Siberian weasel	D	15	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
M. sibirica	Siberian weasel	D	40	Khabarovskii krai	Russia	Kontrimavichus, 1985	49.31	136.53
M. sibirica	Siberian weasel	D	27	Primorskii krai	Russia	Kontrimavichus, 1985	46.00	134.00
M. sibirica	Siberian weasel	D	35	Sikhote-Alin' Preserve	Russia	Kontrimavichus, 1985	45.20	136.50
M. sibirica	Siberian weasel	D	9	Tuva	Russia	Kontrimavichus, 1985	51.50	95.00
Neovison vison	American mink	D	6	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
N. vison	American mink	D	78	Chena River, Fairbanks	U.S.	Swartz, 1968	64.83	−147.70
N. vison	American mink	D	42	Khabarovskii krai	Russia	Kontrimavichus, 1985	51.20	136.74
N. vison	American mink	D	99	Mitkof Is., AK	U.S.	This study	56.68	−132.92
N. vison	American mink	D	28	Primorskii krai	Russia	Kontrimavichus, 1985	46.00	134.00
N. vison	American mink	D	36	Sikhote-Alin' Preserve	Russia	Kontrimavichus, 1985	45.20	136.50
N. vison	American mink	D	25	Yakutia	Russia	Kontrimavichus, 1985	60.00	121.00
N. vison	American mink	D	54	Chelomdzha River, Magadan	Russia	Domnich and Obushenkov, 1983	60.27	147.61
Nyctereutes procyonoides	Raccoon dog	D	31	Khabarovskii krai	Russia	Kontrimavichus, 1985	48.80	135.45
Prionailurus bengalensis euptilurus	Leopard cat	D	37	Sikhote-Alin' Preserve	Russia	Kontrimavichus, 1985	45.20	136.50
Vulpes vulpes	Red fox	D	32	Khabarovskii krai	Russia	Kontrimavichus, 1985	48.80	135.45
V. vulpes	Red fox	D	38	Sikhote-Alin' Preserve	Russia	Kontrimavichus, 1985	45.20	136.50
V. vulpes	Red fox	D	19	Trans Baikal region	Russia	Kontrimavichus, 1985	53.00	107.67
V. v. beringiana	Red fox	D	65	Kamchatka Cape of Lopatka	Russia	Petrov, 1930	50.86	156.68
V. v. daurica	Daurian fox	D	16	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
Myodes rufocanus	Gray red-backed vole	P	7	Tomskaya Oblast	Russia	Karpenko et al., 1998	56.46	84.96
Sorex caecutiens	Laxmann's shrew	P	58	Magadan (Snow Valley)	Russia	Dominch, 1982; this study	59.73	150.87
S. caecutiens	Laxmann's shrew	P	50	Okhotsk village	Russia	This study	59.37	143.35
S. caecutiens	Laxmann's shrew	P	55	Talon village	Russia	This study	59.75	148.65
S. caecutiens	Laxmann's shrew	P	63	Buyunda River, Magadan	Russia	This study	62.43	153.34
S. caecutiens	Laxmann's shrew	P	44	Bol'shoy Shantar Is.	Russia	This study	54.87	137.49
S. caecutiens	Laxmann's shrew	P	30	Lazovski Nature Preserve	Russia	This study	43.26	134.24
S. camtschaticus	Kamchatka shrew	P	59	Magadan (Snow Valley)	Russia	Dokuchaev, 2003	59.73	150.87
S. cinereus	Cinereus shrew	P	81	Alaska	U.S.	This study	65.44	−142.44

APPENDIX. Continued.

Host	Common name	Role	ID	Locality	Country	Author/Data source	Latitude	Longitude
S. cinereus	Cinereus shrew	P	85	Chichagof Is., AK	U.S.	Karpenko et al., 2007	57.41	−135.71
S. cinereus	Cinereus shrew	P	72	Togiak NWR	U.S.	Karpenko et al., 2007	59.05	−160.37
S. cinereus	Cinereus shrew	P	82	Yukon-Charley Rivers N P	U.S.	Karpenko et al., 2007	63.83	−142.16
S. daphaenodon	Siberian large-toothed shrew	P	33	Khabarovskii krai	Russia	Karpenko, 1985	51.67	135.74
S. daphaenodon	Siberian large-toothed shrew	P	60	Magadan (Snow Valley)	Russia	Dominch, 1982	59.73	150.87
S. gracillimus	Slender shrew	P	61	Magadan (Snow Valley)	Russia	Dokuchaev, 2003	59.73	150.87
S. gracillimus	Slender shrew	P	51	Okhotsk village	Russia	This study	59.37	143.35
S. isodon	Taiga shrew	P	52	Okhotsk village	Russia	This study	59.37	143.35
S. isodon	Taiga shrew	P	57	Magadan	Russia	Dominch, 1982	59.63	150.83
S. isodon	Taiga shrew	P	62	Magadan (Snow Valley)	Russia	This study	59.73	150.87
S. isodon	Taiga shrew	P	56	Talon village	Russia	This study	59.75	148.65
S. isodon	Taiga shrew	P	64	Buyunda R., Magadan	Russia	This study	62.43	153.34
S. isodon	Taiga shrew	P	45	Bol'shoy Shantar Is.	Russia	This study	54.87	137.49
S. tundrensis	Tundra shrew	P	73	Togiak NWR	U.S.	This study	59.05	−160.37
S. tundrensis	Tundra shrew	P	83	Yukon-Charley Rivers National Preserve	U.S.	Karpenko et al., 2007	63.83	−142.16
S. unguiculatus	Long-clawed shrew	P	29	Lazovski Nature Preserve	Russia	This study	43.28	134.05
S. unguiculatus	Long-clawed shrew	P	34	Khabarovskii krai	Russia	This study	48.14	136.35
S. unguiculatus	Long-clawed shrew	P	47	Sakhalin Is.	Russia	Dokuchaev, 2003	50.84	142.65
S. unguiculatus	Long-clawed shrew	P	48	Sakhalin Is.	Russia	This study	47.24	142.77

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Phylogeography of a Holarctic nematode, *Soboliphyme baturini*, among mustelids: climate change, episodic colonization, and diversification in a complex host–parasite system

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Phylogeography of *Soboliphyme baturini*, a nematode parasite in mustelids, is explored across Beringia. Sequences of the mitochondrial cytochrome *c* oxidase subunit I and nicotinamide adenine dinucleotide dehydrogenase subunit 4 genes were evaluated from 37 *S. baturini*, representing 19 localities throughout Alaska, Canada, and Siberia. A total of 30 haplotypes was recovered and maximum parsimony and Bayesian phylogenetic analyses support the recognition of a single species with a distribution extending from the Palearctic to the Nearctic. Within *S. baturini*, a host-specific partition in North America between *Martes caurina* and *Martes americana* was not identified. Instead, substantial geographic structure within *S. baturini* relates to the dynamic geological history of this northern region and especially the North Pacific Coast. Beringia and other coastal refugia along the western margin of North America played a large role during stadial maxima in the persistence and divergence of the parasite. Repeated events for biotic expansion and geographic colonization across the Bering Land Bridge and the Holarctic during glacial maxima in the Pleistocene appear to have facilitated at least two episodes of host-switching of this nematode among mustelids in populations now distributed in eastern Beringia. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **96**, 651–663.

ADDITIONAL KEYWORDS: Alaska – Beringia – Canada – COI – *Martes* – ND4 – Siberia.

INTRODUCTION

Few phylogeographic studies of parasites have been initiated relative to free-living organisms, perhaps due to the relatively few parasitologists working in the field of molecular ecology and the generally poor availability of molecular markers and suitable specimens for most parasitic organisms (Criscione, Poulin & Blouin, 2005). Notwithstanding, parasites are ubiquitous and can provide new insights into the basic questions in evolutionary ecology, including attempts to understand the impact of dynamic range expansion due to changing climatic conditions (Hoberg & Brooks, 2008). Phylogeographic assessments of parasites can be particularly informative when placed within the context of host phylogeography. In

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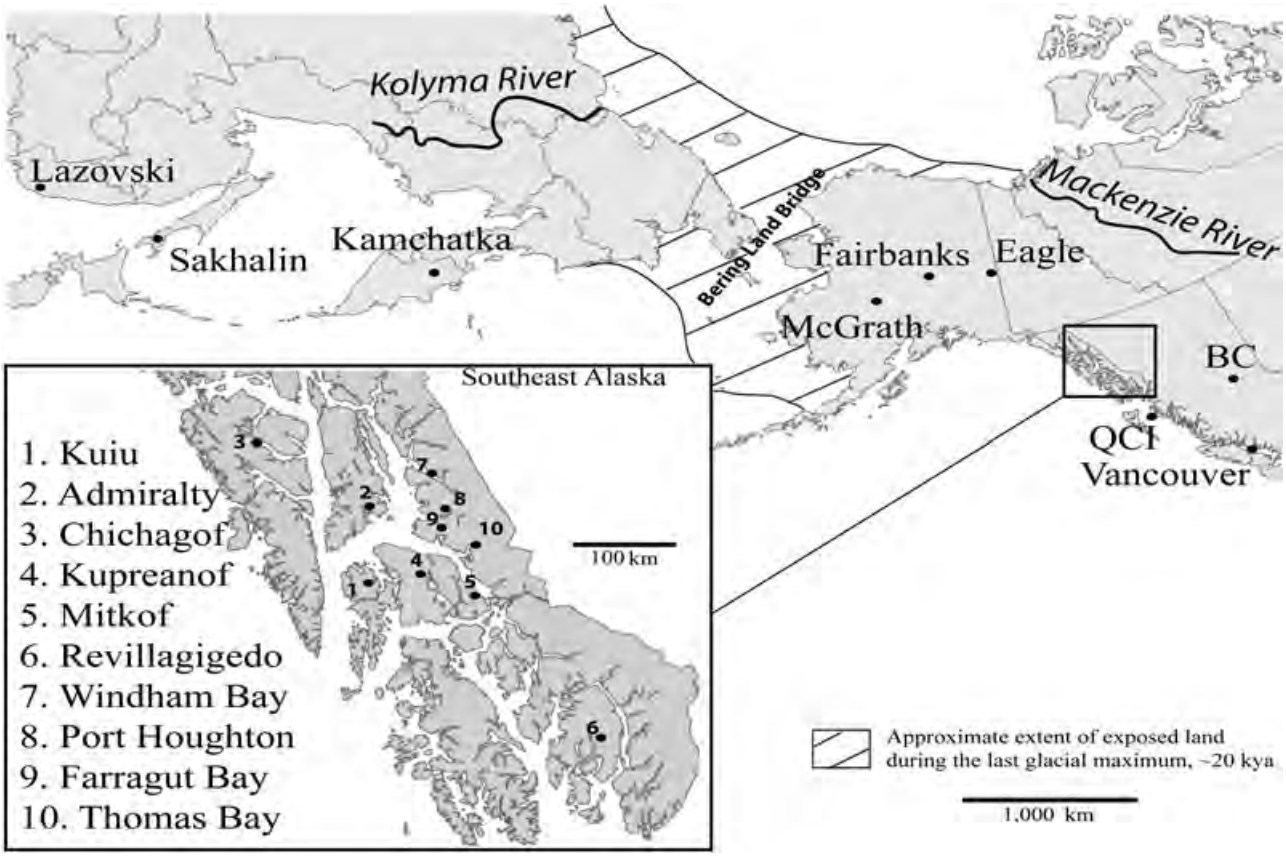

Figure 1. Map of sampling localities for collections of mustelids and *Soboliphyme baturini* in Beringia. Sea levels dropped over 100 m, exposing the continental shelf and creating the 1800 km wide Bering Land Bridge, connecting Paleartic and Nearctic faunas (Hopkins, 1959). Beringia served as an episodic corridor for expansion and isolation of the northern fauna from the Pliocene into the Quaternary. The inset shows detail of localities in Southeast Alaska. BC, British Columbia; QCI, Queen Charlotte Islands.

particular, such a comparative approach can provide insight into episodes of host-switching due to newly-arrived hosts or 'cryptic isolating events', where geographic isolation of hosts creates divergence in parasite populations and serves as a driver for diversification (Hoberg, 1995). Parasites may serve as historical indicators for communities that have responded to dynamic geologic upheaval, such as those experienced by high latitude biota during the Quaternary (Hoberg, 1997). Nieberding *et al.* (2004) extended this concept to the population level and illustrated that parasite phylogeography can provide an independent perspective on community assembly and reveal cryptic events that are not evident when viewed solely from the phylogeography of free living organisms. These observations set the stage to explore the history of an assemblage of mustelid hosts and a parasitic nematode to refine our understanding of the role of climate change in shaping community structure in the Holarctic (Rausch, 1994).

Beringia, the high latitude region between the Kolyma River in Siberia and Mackenzie River in the Northwest Territories, played a pivotal role in habitat continuity and faunal diversification in holarctic biomes (Fig. 1) (Hultén, 1937; Rausch, 1994). Episodic fluctuations in the expansion and contraction of the ice-sheets and concurrent eustatic variation in sea level during the late Pliocene (5.4–2.4 Mya) and Quaternary (2 Mya) shaped contemporary faunal diversity through alternating cycles of biotic expansion and isolation at intercontinental and regional spatial scales, and through the development of local refugia across Beringia (Hopkins, 1959; Hoberg, 1992; Sher, 1999; Lister, 2004). In addition to Beringia's role in biotic diversification, the region served as the primary corridor linking Asian and North American faunas (Rausch, 1994; Elias, Short & Birks, 1996; Hoberg, 2005a) on more than 20 occasions during the Quaternary when the land bridge was exposed.

The study of biotic interchange between continents was pioneered by Simpson (1940). Detailed phylogeographic investigations of a variety of faunal and floral elements (Abbott & Brochmann, 2003; Cook *et al.*, 2005; Waltari *et al.*, 2007) are beginning to provide new perspectives on the extent and timing of intercontinental exchange across this high latitude linkage.

Just beyond the southeastern limit of Beringia, phylogeographic studies of terrestrial mammals along the North Pacific Coast of North America have demonstrated a significant phylogeographic structure that likely reflects a complex history of diversification and geographic colonization linked both to Beringia and regions south of the Nearctic (Lessa, Cook & Patton, 2003). Cyclical stadial–interstadial periods promoted repeated expansion, isolation, and divergence or, in other cases, extinction of high latitude organisms (Cook *et al.*, 2001; Guthrie, 2006; Hoberg & Brooks, 2008). In the Pacific Northwest, for example, several species can be further divided into western coastal and eastern continental forms that apparently reflect deep vicariant events that left a strong molecular signature on the biota (Cook, Dawson & MacDonald, 2006).

The generality of the coastal/continental split now has been documented using molecular genetics across a variety of terrestrial mammals, ranging from soricomorphs, such as the dusky shrew (two deep clades of *Sorex monticolus* Merriam; Demboski & Cook, 2001), to meso-carnivores [sister species, *Martes americana* (Turton) and *Martes caurina* (Merriam); Small, Stone & Cook, 2003], to large carnivores such as black bear (two shallow clades of *Ursus americanus* Pallas; Stone & Cook, 2000; Peacock, 2004).

Each of these mammals also supports a rich parasite fauna and these parasites are now being explored from molecular and morphological perspectives. Consequently, Beringia and surrounding areas provide an ideal setting to test fundamental ideas related to geographic colonization and diversification of host/parasite systems in a region that has experienced substantial climate change and episodic ecological perturbation on varying temporal and spatial scales (Hoberg *et al.*, 2003). Already, molecular investigations of parasites have provided new insights into processes of diversification and historical biogeography for high-latitude hosts (Hoberg *et al.*, 1999; Wickström *et al.*, 2003; Haukisalmi, Henttonen and Hardman, 2006; Haukisalmi *et al.*, 2008).

We examine aspects of Beringian biogeography through phylogeographic studies of *Soboliphyme baturini* Petrow, a stomach dwelling nematode of mustelids found primarily in sable [*Martes zibellina* (Linnaeus)], American marten (*M. americana*), and Pacific marten (*M. caurina*). Distribution of *S. baturini* is centered in the amphi-Beringian region extending from central Siberia to the Pacific Northwest of North America (Koehler *et al.*, 2007). This relatively widespread nematode provides an opportunity to test previous hypotheses related to the diversification of its primary mustelid hosts (Anderson, 1994; Carr & Hicks, 1997; Stone & Cook, 2002; Stone, Flynn & Cook, 2002; Small *et al.*, 2003) and we explore the evolutionary history of *S. baturini* in light of the dynamic geologic events that characterized high latitudes during the Quaternary. We amplify and address the following questions: (1) what is the biogeographic history for *S. baturini* across Beringia and to what degree have episodic events in the Pleistocene influenced patterns of host association; (2) in North America, is *S. baturini* genetically partitioned between the two primary mustelid hosts, *M. americana* (continental) and *M. caurina* (coastal); and (3) how has this parasite responded to the arrival of novel potential hosts following glacial retreat in these high latitude regions during the post-Pleistocene?

MATERIAL AND METHODS

Specimens

In conjunction with the Beringian Coevolution Project (Hoberg *et al.*, 2003; Cook *et al.*, 2005), adult and juvenile specimens of *S. baturini* were obtained from 19 geographic sites across eastern Siberia and the Pacific Northwest (see Supporting information, Appendix S1) (Koehler *et al.*, 2007). Adult nematodes from North American localities were acquired through necropsies of mustelid carcasses salvaged from commercial trappers. Other samples of *S. baturini*, including juvenile specimens from soricomorphs (e.g. shrews of the genus *Sorex*), were obtained through collaborative efforts. A complex life cycle characterizes *S. baturini*. Adult nematodes mature in the stomach of the definitive host and females release eggs that are shed in feces and deposited in the soil. Eggs are eaten by enchytraeid oligochaetes (intermediate host) in the leaf litter, and juvenile nematodes develop to the infective juvenile (J_3) stage that is then transmitted to mammals (Karmanova, 1986). Shrews and rodents feed on these oligochaetes and may serve as paratenic hosts that bridge the trophic gap between mustelid and oligochaete, or the nematode may infect the definitive hosts directly through the consumption of enchytraeids (Karpenko, Dokuchaev & Hoberg, 2007; Koehler *et al.*, 2007). Therefore, at any particular locality, populations of this nematode may occur in several species of mustelids or soricomorphs and, regardless of host, may exhibit minimal genetic variation (Koehler *et al.*, 2007).

Specimens from Kamchatka, Russia (Kamchatkan Peninsula) lacked precise locality data. Adult specimens of *Soboliphyme jamesoni* Read (1952) were collected from *Sorex tundrensis* Merriam and *Sorex roboratus* Hollister near Yakutsk, Russia. Adult specimens of adult *Soboliphyme abei* Asakawa in a long-clawed shrew (*Sorex unguiculatus* Dobson) were from Hokkaido, Japan (see Supporting information, Appendix S1). Nematodes were preserved in 70% or 95% ethanol and stored at –20 °C. Each specimen was subsampled, with the mid-section of the body being reserved for molecular sequencing, whereas the head and tail of individuals were archived as physical vouchers deposited in the Museum of Southwestern Biology (see Supporting information, Appendix S1).

Molecular techniques

Adult and juveniles, totaling 37 individual specimens, of *S. baturini* (Fig. 1; see also Supporting information, Appendix S1) were sequenced. Additionally, one specimen each of *S. abei* and *S. jamesoni* was sequenced. Total genomic DNA was extracted from individual worms using a commercial kit (AquaPure Genomic DNA isolation kit, Bio-Rad Laboratories). A 351-bp region of the nicotinamide adenine dinucleotide dehydrogenase subunit 4 (ND4) mitochondrial gene was amplified by polymerase chain reaction (PCR) using the primer pair SoboND4F 5′-GGGAGGGCCACTT ACCTTAT-3′ and SoboND4R 5′-GCCACAAACTTC TTCACGTCT-3′. The ND4 gene is well suited for identifying morphologically cryptic species and resolving intraspecific phylogenies (Blouin, 2002). A 293-bp region of cytochrome *c* oxidase subunit I (COI) was amplified with the primers SoboCOIF 5′-GCTCA GCTTCGGACAGTTTC-3′ and SoboCOIR 5′-TCATGC AAATGAACATCTAGGG-3′ (Tran, 2003). PCR products were sequenced using methods described in Koehler *et al.* (2007). Annealing temperatures were 53 °C (COI) and 67 °C (ND4) for 15 s.

Forward and reverse strands were sequenced using an ABI PRISM® 3100 genetic analyser. Ambiguous sites were resolved using SEQUENCHER, version 4.6 (Genecodes). Alignments were made with CLUSTALW (Chenna *et al.*, 2003). Mitochondrial sequences were translated to amino acids and examined for stop codons to identify potential pseudogenes. Sequences were deposited in GenBank and linked to physical vouchers deposited in the Museum of Southwestern Biology.

Data analysis

Phylogenetic analyses were performed to examine relationships among *S. baturini* from 19 distinct geographic regions. DnaSP (Rozas & Rozas, 1999) was used to generate and analyse the haplotype matrices and estimate haplotype and nucleotide diversity (using uncorrected *p* values). ARLEQUIN, version 3.11 (Excoffier, Laval & Schneider, 2005) generated measures of genetic divergence (F_{ST}) using pairwise comparisons. Separate sequences of ND4 and COI were run with MODELTEST, version 3.06 (Posada & Crandall, 1998) and PAUP* 4.0b (Swofford, 2002) to determine the nucleotide substitution models best for the partitioned Bayesian matrix (Ronquist & Huelsenbeck, 2003). ND4 was best fit with the HKY+G model and COI was best fit with the TVM+G model. Five million generations were run with four heated chains. Trees were generated every 100 generations. Burn in was set at 5000 trees, leaving 45 000 trees to construct 50% majority consensus trees and posterior probabilities. Bayesian analyses were run several times to ensure convergence and insensitivity to priors.

Trees generated from maximum parsimony (MP), minimum evolution (ME), and Bayesian analyses were initially unrooted. Alignments for sequences of *S. baturini* with either *S. abei* or *S. jamesoni* were equivocal due to a high level of heterogeneity and apparently distant evolutionary relationship of these outgroups. Population level analyses were instead rooted based on explicit assumptions about biogeographic origins and temporal criteria as outlined below. MP and Neighbour-joining algorithms were also run with sequences that were translated to amino acids or with the third position of the codons only. The median-joining algorithm (Bandelt, Forster & Röhl, 1999) in the program NETWORK, version 4.1.1.2 (Fluxus Engineering) was used to create a haplotype network that was subsequently superimposed over a map of the region created using ArcGIS, version 9.0 (ESRI).

RESULTS

The COI matrix contains 293 bp (14 variable, six parsimony informative). The transition/transversion (ti/tv) ratio is 4.02 and nucleotide frequencies are A = 19.67%, C = 13.76%, G = 23.73%, and T = 42.83%. The ND4 matrix contains 351 bp (44 variable, 30 parsimony informative) with ti/tv of 7.08 and nucleotide frequencies are A = 25.12%, C = 8.02%, G = 37.83%, and T = 29.03%.

Geographic distributions and phylogeography

Clear partitions among populations of *S. baturini* across Beringia were demonstrated based on combined sequences of ND4 and COI (647 bp) and 30 haplotypes assessed in Bayesian analyses (Fig. 2). Three primary clans (Wilkinson *et al.*, 2007) were

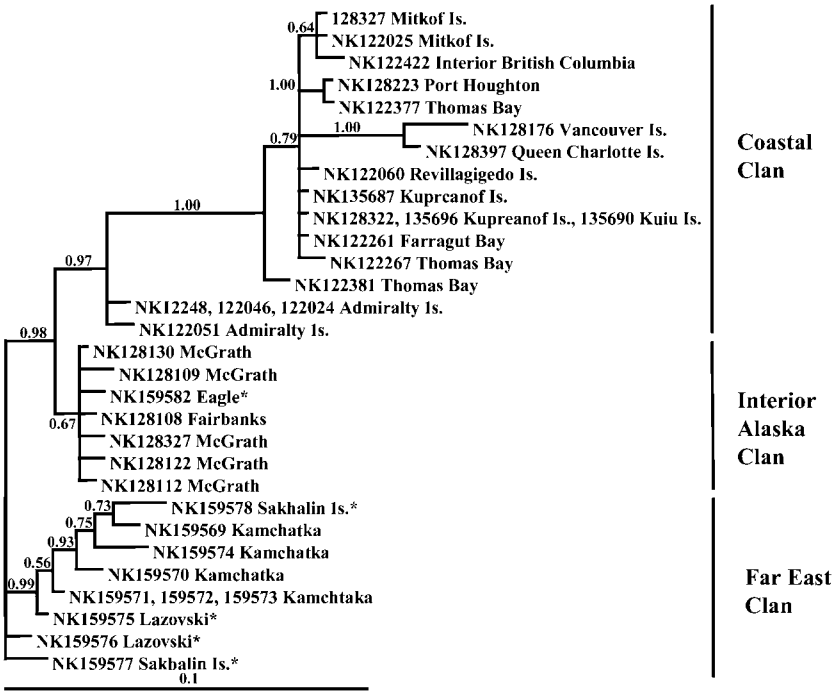

Figure 2. Phylogenetic relationships of *Soboliphyme baturini* based on a Bayesian inference (unrooted). Analysis is based on a combined dataset for nicotinamide adenine dinucleotide dehydrogenase subunit 4 (351 bp) and cytochrome *c* oxidase subunit I (293) using a GTR + I evolutionary model. Posterior probabilities are listed adjacent to nodes. Tree is unrooted. Major and minor subdivisions are illustrated. *Soricomorph host.

identified: Russia, Interior Alaska and Coastal Alaska, and British Columbia. Two Russian samples form a basal polytomy to all samples. Within the coastal clan Admiralty Island samples are basal and substantial partitions are also evident relative to Vancouver and Queen Charlotte Islands. By contrast, minimal structure and divergence is indicated within populations in Interior Alaska or within the Alaskan coastal zone and Interior British Columbia populations.

MP, ME and Bayesian trees (not shown) that explored geographic variation among populations of *S. baturini* were rooted with *S. abei* and *S. jamesoni*. None of these trees was explicit in revealing basal or ancestral geographic associations for *S. baturini* and all analyses were associated with low support values and conflicting topologies. For these genes, *S. abei* and *S. jamesoni* appear to be too divergent (average divergence 27% ND4 and 21% COI) from *S. baturini* to reliably be used as outgroups. Hence, these data were insufficient for determining the directionality of expansion events across Beringia.

Secondary criteria based on assumptions about historical biogeography were applied to provide an alternative justification to root trees for populations of *S. baturini*. Within the genus *Soboliphyme*, seven of nine species are endemic to Eurasia, so this region was postulated as the ancestral range for Soboliphymatidae. These criteria are consistent with origins in Eurasia for *S. baturini* and constitute the justification to specify a population from the Russian Far East as basal for purposes of establishing a root for population-level analyses.

Patterns of intraspecific molecular diversity

Haplotype diversity of the combined COI and ND4 genes was high in each of the three regions (Table 1), whereas nucleotide diversity was higher for both Coastal and Far East clans and lowest for interior Alaska. Overall genetic divergence was lowest in Interior Alaska and highest in the Coastal clan. Within the later, the three insular populations found in *M. caurina* (Admiralty, Queen Charlotte Islands, Vancouver) were the most divergent.

The haplotype network (Fig. 3) reveals three major clans (Asian, Interior Alaskan, and Coastal) that correspond to discrete geographic regions and reflect the contrast between nucleotide and haplotype diversity. This network has a 'dumbbell' shape that reflects higher levels of diversity and divergence on the western (Russia) and southeastern edges (North Pacific Coast) of the distribution. Deeper divergence contrasts with a relatively shallow star topology

Table 1. Genetic variation for the combined cytochrome *c* oxidase subunit I (293 bp) and nicotinamide adenine dinucleotide dehydrogenase subunit 4 (351 bp) genes

Group	Sample size	Number of haplotypes	Genetic divergence	Nucleotide diversity	Haplotype diversity
Interior Alaska	7	7	2.57	0.0049	1.0000
Coastal	20	15	8.79	0.0156	0.9632
Far East	10	8	5.73	0.0109	0.9333
All	37	30	–	0.0262	0.9850

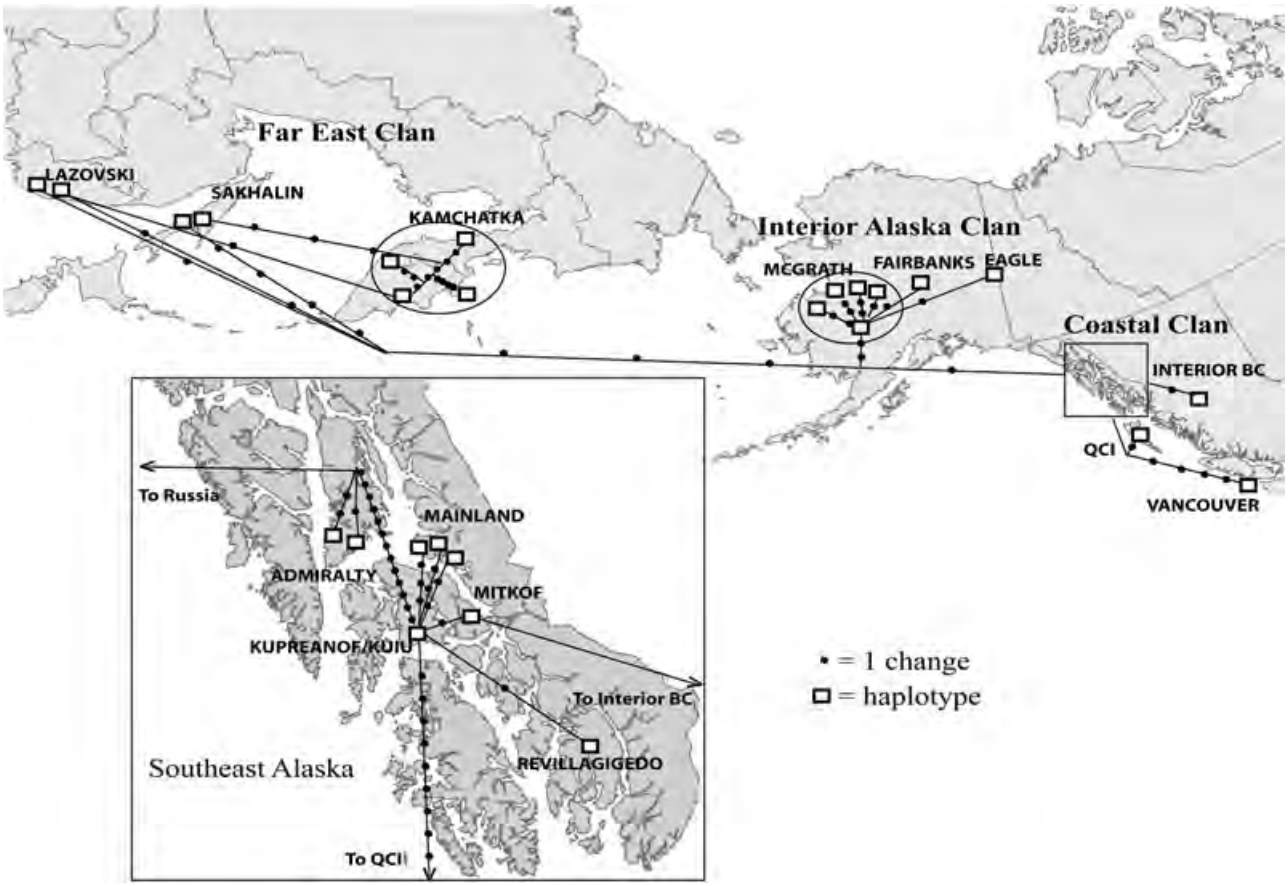

Figure 3. Median-joining network for populations and haplotypes of *Soboliphyme baturini* in Beringia. Asian, Interior Alaskan, and Coastal clans are indicated. Relationships have been inferred for 351 bp of nicotinamide adenine dinucleotide dehydrogenase subunit 4 and 293 bp of cytochrome *c* oxidase subunit I. Black dots represent individual mutations between haplotypes. Inset shows the details for populations distributed in Southeast Alaska; localities are approximated. Encircled haplotypes indicate that specimens are from the same general locality.

found in the Interior clan; a clan comprised of individuals that are centrally located in the geographic range of *S. baturini*.

DISCUSSION

Macroparasites serve as fine-scale and independent indicators of biogeographic history for their associated hosts by linking events in evolutionary and ecological time (Brooks & McLennan, 1993, 2002; Hoberg & Klassen, 2002; Hoberg & Brooks, 2008). Our exploration of *S. baturini* across Beringia reveals a complex history of biotic expansion involving substantial geographic and host colonization consistent with a broader process for taxon pulses that have structured this fauna (Hoberg & Brooks, 2008). In North

America, refugial effects in the parasite are tied primarily to purported paleoendemic populations of *M. caurina* (Small *et al.*, 2003), whereas only recent, independent colonizations of *M. americana* are postulated in locations where this marten is a relative newcomer. Geographic structure in this host–parasite system is greatest across the islands of the North Pacific Coast that support *M. caurina*. Lowest geographic divergence is found among nematodes that inhabit *M. americana*, including populations along the North Pacific Coast (both island and mainland) and populations in Interior Alaska. Within marten, at least two events of host-switching by this nematode are evident. Independent colonizations in the Holocene of *M. americana* occurred once after this host arrived in Interior Alaska and then again in coastal southeast Alaska as *M. americana* colonized this region after deglaciation of the mainland and corridors through the Coastal Range (e.g. Stikine River).

History of a Beringian nematode, *S. baturini*

Whether faunal exchange between Asia and North America during the Pleistocene was symmetric has long been debated (Simpson, 1940; Rausch, 1994). Waltari *et al.* (2007) examined the overall trend in patterns of geographic colonization based on phylogeographic analyses and found nine of 14 organisms showing eastward expansion across the Bering Land Bridge. Studies on cestodes of arvicoline rodents (Haukisalmi *et al.*, 2001, 2002, 2006, 2008; Wickström *et al.*, 2003) and nematodes among lagomorphs and artiodactyls (Hoberg, 2005a) also reported eastward expansion from the Palearctic. This eastward colonizing trend likely relates to differential availability of source populations. Western Beringia had a porous border with central Asia during full glacial events (Anderson & Borns, 1997), whereas eastern Beringia was completely isolated from the remainder of North America (Rausch, 1994).

Phylogenetic analyses based on the nuclear small subunit 18S gene and mitochondrial COI gene have indicated that the genus *Soboliphyme* is sister to other Dioctophymida among the basal zooparasitic nematodes (Rusin *et al.*, 2003; Koehler, 2006; Meldal *et al.*, 2006). *Soboliphyme baturini* represents a single widespread species and shares a sister-group relationship with an assemblage of eight other *Soboliphyme* spp. that is otherwise only associated with soricimorph hosts (Ribas & Casanova, 2004; Koehler *et al.*, 2007). Only one of these, *S. jamesoni*, is also found in North America in the shrew, *Sorex vagrans* Baird (Read, 1952). Primarily a parasite in mustelids, *S. baturini* also has been reported in 31 other species of mammals, although most are either incidental definitive hosts or paratenic hosts. This nematode apparently readily switches among marten (*M. americana*, *M. caurina*), ermine (*M. erminea* Linnaeus), or mink (*N. vison* (Schreber)) at any particular locality throughout its geographic range in North America. *Martes* spp., however, may represent the primary source for nematodes across this broader array of mustelids (Koehler *et al.*, 2007). Among mustelid definitive hosts, the highest prevalence for *S. baturini* has been reported in *Martes* spp. from Siberia and Southeast Alaska (Kontrimavichus, 1985; Karmanova, 1986; Zarnke *et al.*, 2004).

Molecular variation across the geographic range of *S. baturini* is essentially partitioned into three primary clans (Asian, Interior Alaska, and Pacific Coastal). Although individual clans for populations of *S. baturini* were supported, a basal clade could not be unequivocally identified when either *S. abei* or *S. jamesoni* were included as outgroups. Consequently, at this time, the direction of interhemispheric colonization of *S. baturini* is equivocal, All nine species of *Soboliphyme*, except *S. baturini*, are found as adults in soricimorphs. The relationship of *S. baturini* to the remaining species of *Soboliphyme* has a direct bearing on interpretation of the timing of putative host switches between mustelids and soricimorphs. If *S. baturini* diverged early in the history of the Soboliphymatidae (or is the sister for an assemblage of species in soricimorphs), then all the extant, soricimorph-dwelling species of *Soboliphyme* may be too divergent for the purpose of rooting with this set of molecular markers.

Our leading hypothesis regarding the directionality of colonization between Asia and North America favors an eastward expansion for *S. baturini* along with the ancestor to *M. americana/caurina*. Two species of *Soboliphyme* are Holarctic, whereas the other seven are endemic to the Palearctic, perhaps lending support to a Palearctic origin. The presence of *Soboliphyme* in the Nearctic would then be consistent with independent colonization of North America by the Holarctic species, *S. jamesoni* (in shrews of the genus *Sorex*) and *S. baturini* (in *Martes*), during the Pleistocene. Host-switching between shrews and mustelids by an ancestral *Soboliphyme* would have occurred in the Palearctic. Geographic colonization of *S. baturini* extending eastward across the Bering Land Bridge coincided with expansion for the ancestral form of *M. americana/caurina* that apparently entered North America 65–122 Kya (Anderson, 1994) in the mid-Wisconsin. Subsequent and sequential geographic colonization along the coastal archipelago, mediated by *M. caurina*, may have occurred along the Pacific Coast west of the Coastal Range to south of Washington and later east to Wyoming (Fig. 3).

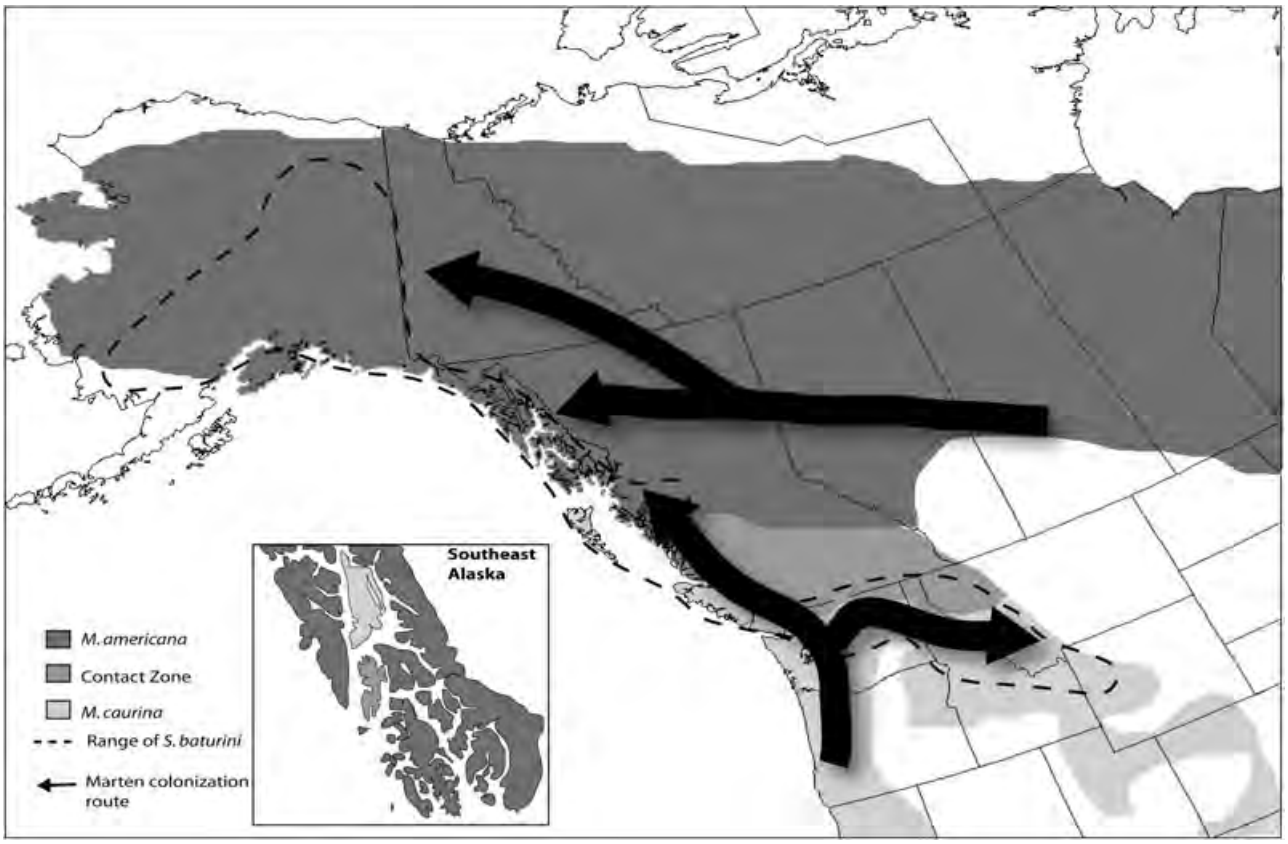

Figure 4. Distribution of *Soboliphyme baturini*, *Martes americana*, and *Martes caurina* in North America (*sensu* Koehler *et al.*, 2007). Arrows indicate proposed routes of migration following the latest glacial retreat.

Low levels of genetic differentiation in coastal populations would be predicted if distributions represent a more recent (last glacial maximum, 15 Kya) eastward expansion from Asia because these populations would be the most recently founded. Conversely, an older expansion, consistent with the first entry of marten into North America (65–122 Kya; Anderson, 1994) might be reflected by deeper interpopulation divergence. Indeed, high levels of divergence characterize the Coastal clan of *S. baturini* and likely reflect the long-term persistence of these insular populations. These highly-divergent populations may be attributed to the existence of ice-free refugia in the Alexander Archipelago during the late Wisconsin as has been proposed based on geologic evidence (Carrara, Ager & Baichtal, 2007) and phylogeographic studies of other mammals (Fleming & Cook, 2002; Cook *et al.*, 2006).

If *S. baturini* occurred in the ancestor of *M. caurina* and *M. americana* that originally colonized North America, the parasite may have been subsequently lost (Paterson & Gray, 1997) in *M. americana* when isolated in an eastern continental refugium in North America during the late Pleistocene. *Martes americana* later acquired (or re-acquired) *S. baturini* from *M. caurina* or other mustelids when the Pacific Coast marten colonized the Pacific Coast (Fig. 4) in the Holocene (Small *et al.*, 2003). Farther north, *M. americana* independently expanded westward, tracking degalciation into interior Alaska during the Holocene (Graham & Graham, 1994), where *S. baturini* may have been acquired from other mustelids that persisted there during the Pleistocene, such as wolverine (*Gulo gulo* (Linnaeus) or the extinct *M. nobilis*, whose fossils may actually represent large *M. caurina* (Al-Suwaidi *et al.*, 2006). In Asia, sable (*M. zibellina*) were considered to be a valued furbearer for over 2000 years but were almost exterminated by the 1600s (Bakeyev & Sinitsyn, 1994; Ma & Xu, 1994). Efforts to restore populations began in the 1940s, resulting in the translocation throughout Russia of over 18 500 *M. zibellina* from Kamchatkan and Buryatian (near Lake Baikal) source populations (Monakhov, 2001). That history of deliberate introductions combined with our limited sampling in Asia precludes a rigorous exploration of phylogeographic variation of *S. baturini* in eastern Asia. Nevertheless, significant phylogeographic structure uncovered for this nematode in Asia appears to contradict the

purported widespread extirpation of the sable followed by introduction from a limited number of source populations. Hence, genetic and morphological studies suggest that geographic structure in Kamchatkan sable was not entirely influenced by human translocations (Balmysheva & Solovenchuk, 1999a, b; Monakhov, 2001; Dubinin & Valentsev, 2003).

Molecular geographic variation in a few other parasitic helminths has been explored across this region. For example, at a deeper temporal scale, *Trichinella* spp. demonstrate multiple expansion events from Eurasia to the Nearctic with carnivore hosts including mustelids coinciding with different glacial maxima during the Pleistocene (Zarlenga *et al.*, 2006). Speciation events for *Trichinella* were also apparently driven by sequential episodes of biotic expansion and isolation in the context of stadial–interstadial cycles. *Soboliphyme baturini* contrasts with this system suggesting instead an instance where parasites may have failed to speciate (Brooks & McLennan, 1991; Johnson *et al.*, 2003; Hoberg, 2005b) in geographic isolation along the North Pacific Coast and habitats south of the Laurentide–Cordillera ice sheets.

In North America, does *S. baturini* reflect the coastal/continental split of its hosts

Cospeciation or recent host colonization events (i.e. host-switching) comprise two possible hypotheses that may account for the distribution of *S. baturini* among a variety of mustelid hosts, but these mechanisms produce different expectations. First, if cospeciation was the primary mechanism, then one would expect parasite lineage partitioning specific to each mustelid species that it inhabits. If this host–parasite association extends back to the origin of this Holarctic mustelid clade, then the absence of *S. baturini* in the European mustelids, *Martes foina* Erxleben and *Martes martes* Linnaeus would be the result of 'missing the boat' (Paterson & Gray, 1997) or extinction. Alternatively, the host distribution of this nematode could reflect ecological fitting where the parasite tracks resources in the host, rather than the host itself (Janzen, 1985; Brooks *et al.*, 2006). Preliminary assessment of this nematode/mustelid association indicated rampant host-switching (Koehler *et al.*, 2007) and this expanded analysis also is consistent with the concept of ecological fitting (Hoberg & Brooks, 2008).

Fossil evidence suggests that ancestors of North American marten (*M. americana* and *M. caurina*) diverged from those of the Asian sable, *M. zibellina*, following arrival in the Nearctic via the Bering Land Bridge during the late Pleistocene (65–122 Kya) (Anderson, 1994). *Martes americana* and *M. caurina* are sister to an Asian clade comprised of *M. zibellina*, *M. martes*, and *Martes melampus* Wagner. Microsatellite data, mitochondrial DNA markers, and morphological data support two distinct species of marten in North America (Merriam, 1890; Stone *et al.*, 2002; Cook *et al.*, 2006). Pacific marten likely diverged from an ancestral form when isolated in low latitude coastal refugia during glacial advances in western North America. During the late Pleistocene or early Holocene, populations of Pacific marten apparently recolonized northward along the coast and also eastward to Wyoming (Small *et al.*, 2003), with the distribution of *S. baturini* in North America most closely approximating the Pacific marten. Indeed, deep phylogeographic structure across island nematode populations mirrors that of corresponding insular populations of the Pacific marten.

By contrast, *M. americana*, is thought to have inhabited Pleistocene refugia well east of the Rocky Mountains. During the Holocene, the molecular data suggest that this species expanded north and westward tracking the retreat of Cordilleran and Laurentide ice (Small *et al.*, 2003), a conclusion supported by the fossil record (Graham & Graham, 1994). The fossil record (Anderson, 1994) indicates that *Martes americana*) moved westward across western Canada into eastern Beringia (interior Alaska) within the last 10 000 years (Pielou, 1991: fig. 1.3), thus establishing the Holocene as the period for colonization of these northern Alaska populations by this parasitic nematode. Independent colonization of coastal, southeast Alaska by this eastern marten likely would have occurred even later as ice-free corridors opened through the high coastal mountains linking interior British Columbia with the narrow strip of mainland along coastal Southeast Alaska and British Columbia (Pielou, 1991; Small *et al.*, 2003; MacDonald & Cook, 2007). These independent colonizations of interior Alaska and Southeast Alaska led to at least two independent contacts with *S. baturini*. Hence, only these far western populations of *M. americana* are currently infected with *S. baturini*.

In summary, this nematode/mustelid association was shaped largely by climate and the dynamic geologic history of the Beringian region. Host-switching and geographic colonization served as substantial drivers for contemporary distributions and these patterns are consistent with a developing synthesis linking processes for ecological fitting, oscillation, and taxon pulses as determinants of faunal structure for parasites (Hoberg & Brooks, 2008). Host colonization of *M. americana* by *S. baturini* occurred twice in the Holocene: once upon arrival of *M. americana* in Southeast Alaska and also when *M. americana* colonized interior Alaska in the Holocene. Future studies of this system should investigate DNA sequence variation from independent loci, more extensive

geographic and host sampling of the nematode across this vast region, and more intensive population-level sampling, particularly for the highly-differentiated insular populations along the North Pacific Coast. In addition, a resolved phylogeny for all nominal species of *Soboliphyme* may further clarify our understanding of deeper evolutionary history, including host associations among mustelids and soricimorphs and the direction and timing of faunal exchange across this high latitude nexus.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of *Soboliphyme baturini* specimens included in the phylogenetic tree analyses and network. Nematodes were collected through the Beringian Coevolution Project and other collaborators in the Beringian region. Specimens are listed by Museum of Southwestern Biology NK voucher number, GenBank number, host species, locality and geographic coordinates in decimal degrees. *Sequences from previous study (Koehler *et al.*, 2007). Outgroups ***Soboliphyme abei* ****Soboliphyme jamesoni.*

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Session II: Population Genetics and Evolution

Genetic Relationships Among Chum Salmon Populations in Southeast Alaska and Northern British Columbia

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Kondzela, C.M., C.M. Guthrie, S.L. Hawkins, C.D. Russell, J.H. Helle, and A.J. Gharrett. 1994. Genetic relationships among chum salmon populations in southeast Alaska and northern British Columbia. Can. J. Fish. Aquat. Sci. 51(Suppl. 1): 50–64.

Allozymes from 46 loci were analyzed from chum salmon (*Oncorhynchus keta*) collected at 61 locations in southeast Alaska and northern British Columbia. Of the 42 variable loci, 21 had a common allele frequency <0.95. We observed significant heterogeneity within and among six regional groups: central southeast Alaska, Prince of Wales Island area, southern southeast Alaska – northern British Columbia, north-central British Columbia, and two groups in the Queen Charlotte Islands. Genetic variation among regions was significantly greater than within regions. The three island groups were distinct from each other and from the mainland populations. Allele frequencies were stable over time in 14 of 15 locations sampled for more than 1 yr. The geographic basis for heterogeneity among regions is confounded in part by spawning-time differences. The Prince of Wales and Queen Charlotte populations spawn in the fall; the mainland populations spawn mainly in the summer, although some overlap exists. Overall, most genetic diversity (97%) occurred within sampling locations; the remaining diversity was distributed almost equally within and among regions. Our genetic data may provide fishery managers a means to estimate stock composition in the mixed-stock fisheries near this boundary between the United States and Canada.

Les auteurs ont analysé les allozymes en 46 loci chez des saumons kétas (*Oncorhynchus keta*) prélevés à 61 sites du sud-est de l'Alaska et du nord de la Colombie-Britannique; des 42 loci variables, 21 possédaient une fréquence allélique commune <0,95. Ils ont observé une hétérogénéité significative tant au sein qu'entre les six groupes régionaux suivants : sud-est central de l'Alaska, région de l'Île Prince-William, secteur sud du sud-est de l'Alaska – nord de la Colombie-Britannique, nord-central de la Colombie-Britannique et deux des Îles de la Reine-Charlotte. La variation génétique entre les régions était nettement plus élevée que la variation au sein des régions, tandis que les trois groupes insulaires étaient distincts l'un de l'autre et des populations continentales. Les fréquences alléliques étaient stables dans le temps à 14 des 15 sites échantillonnés pendant plus d'un an. Le fondement géographique de l'hétérogénéité entre les régions est obscurci en partie par des différences liées à la saison de fraie. Les populations de l'Île Prince-William et des îles de la Reine-Charlotte frayent en automne tandis que les populations continentales frayent surtout en été, bien qu'un certain chevauchement existe. En général, la plus grande partie de la diversité génétique (97%) a été notée dans les sites d'échantillonnage tandis que le reste était réparti également entre les régions et dans les régions. Les données génétiques recueillies permettront peut-être aux gestionnaires des pêches d'estimer la composition des stocks faisant l'objet d'une pêche mixte près de la frontière canado–américaine.

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Chum salmon (*Oncorhynchus keta*) spawn in hundreds of streams in southeast Alaska and northern British Columbia. With few exceptions, these chum salmon are wild stocks not enhanced or manipulated by people. They are a major resource in this region, caught in a number of fisheries on both sides of the United States – Canada border. Several fisheries that harvest other species of salmon incidentally catch a substantial number of chum salmon (Clark et al. 1986). Concern about the conservation of chum salmon stocks in the boundary area has arisen because recent annual escapements in this area have been well below target levels or historic averages (Pacific Salmon Commission 1987).

Tagging studies initiated because of this concern have shown that returning adult chum salmon come into the coastal waters between southeast Alaska and northern British Columbia as mixed stocks (Alaska Department of Fish and Game 1986). Generally, they arrive along the southern coast of southeast

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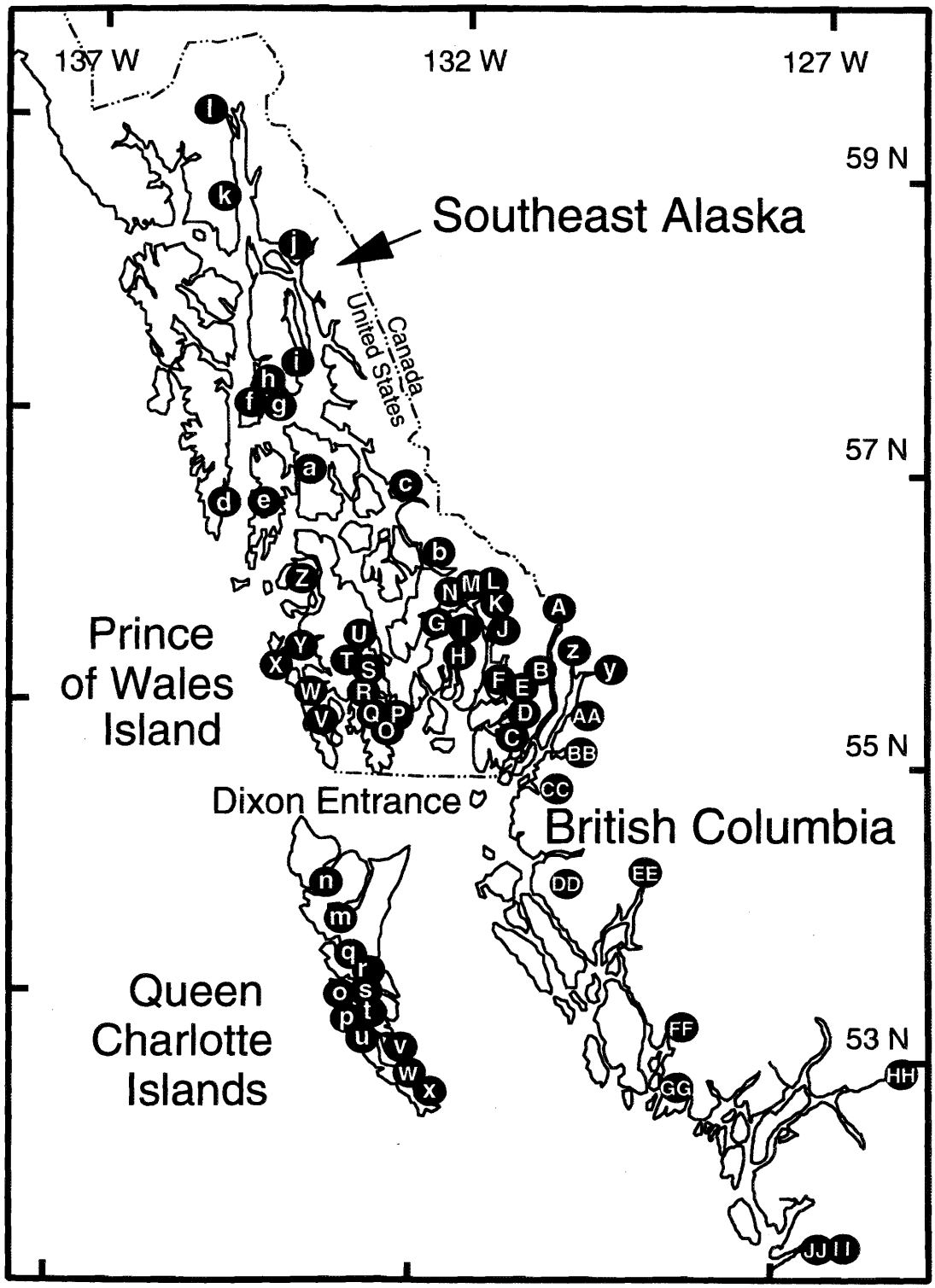

FIG. 1. Locations of chum salmon samples collected in southeast Alaska and northern British Columbia. Letters correspond to location names in Table 1 and Figs. 2 and 3.

Alaska and move into Dixon Entrance before swimming north or south toward their spawning streams. Spawning time, age structure, morphology, and developmental differences have been documented for chum salmon populations throughout their range (Bakkala 1970; Helle 1984; Beacham et al. 1987, 1988; Salo 1991). Several studies have also shown significant genetic variation among chum salmon populations (Okazaki 1981, 1982, 1983; Davis and Olito 1982; Beacham et al. 1985, 1987; Phelps et al. 1994; R. Wilmot, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, AK 99801, personal communication). These studies sampled populations from different areas of the chum salmon range or examined a relatively small number of loci. Except for several populations sampled with a limited number of loci (Davis and Olito 1982), the genetic structure of chum salmon populations in southeast Alaska has not been investigated.

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TABLE 1. Group designation (letters correspond to streams listed in Figs. 1–3, Appendix 1), location, date of collection, and numbers of chum salmon samples used for electrophoretic analysis. Districts are Alaska Department of Fish and Game Statistical Areas. Areas are Canadian Statistical Areas. *N* is number of samples.

Group designation	Location	Date	*N*
	Southeast Alaska		
District 101: Behm Canal – Portland Canal – Boca de Quadra			
A	Fish Creek	5 Sept. 1986	100
		26 Aug. 1987	50
		8 Aug. 1988	100
		25 Sept. 1988	52
B	Tombstone River	10 Aug. 1986	98
C	Marten River	9 Aug. 1986	105
D	Keta River	25 July 1986	101
E	Blossom River	26 July 1986	101
F	Wilson River	8 Aug. 1986	103
G	Traitor's Creek	20 Aug. 1986	101
		22 Aug. 1988	105
H	Carroll River	19 Aug. 1986	100
I	Portage Creek	30 July 1986	111
		22 Aug. 1988	63
J	King Creek	20 July 1986	100
		20 July 1988	52
K	Klahini River	12 Aug. 1986	102
L	Eulachon Creek	13 Aug. 1986	90
M	Grant Creek	14 Aug. 1986	127
N	Herman River	28 July 1986	100
District 102: eastern Prince of Wales Island			
O	Kugel Creek	23 Sept. 1986	104
P	Aiken Creek	22 Sept. 1986	100
Q	Disappearance Creek	21 Sept. 1986	100
		21 Sept. 1988	100
R	Lagoon Creek	20 Sept. 1986	102
S	Old Tom Creek	24 Sept. 1986	100
		22 Sept. 1988	53
T	Cabin Creek	26 Sept. 1986	103
U	Karta River	25 Sept. 1986	100
District 103: western Prince of Wales Island area			
V	Coco Harbor	24 Sept. 1987	100
W	Breezy Bay	12 Sept. 1986	100
		22 Sept. 1987	100
		5 Sept. 1988	54
X	Port Real Marina	10 Sept. 1986	100
		9 Sept. 1988	48
Y	Cruz Cove	8 Sept. 1986	84
		26 Sept. 1987	56
		3 Sept. 1988	54
Z	Tokeen Creek	9 Sept. 1986	101
District 105: western Sumner Strait			
a	Irish Creek	24 Aug. 1986	98
District 107: Ernest Sound – Bradfield Canal			
b	Harding River	22 Aug. 1986	95
District 108: Stikine River			
c	North Arm Creek	10 Aug. 1987	81
District 109: Southern Chatham Strait – western Frederick Sound			
d	Lover's Cove Creek	19 Aug. 1987	100
		16 Aug. 1990	31
e	Elena Bay	25 Aug. 1989	61
f	Eliza Harbor	27 Aug. 1989	61

TABLE 1. (*Concluded*)

Group designation	Location	Date	*N*
District 110: Eastern Frederick Sound			
g	Donkey Creek	25 Aug. 1986	100
		25 Aug. 1990	62
h	Pybus Bay east	28 Aug. 1989	65
i	Gambier Bay southwest	29 Aug. 1989	27
		25 Aug. 1990	40
District 115: Lynn Canal			
k	Lynn Brothers	28 July 1988	50
l	Herman Creek	17 Oct. 1987	100
		22 Sept. 1990	59
	North-central British Columbia		
Area 1: northern Queen Charlotte Islands			
m	Awun River	19 Oct. 1989	75
Area 2: western Queen Charlotte Islands			
n	Mace Creek	mid-Oct. 1989	100
o	Peel Creek	11 Oct. 1989	75
p	Tasu Creek	11 Oct. 1989	100
Area 2: eastern Queen Charlotte Islands			
q	Lagins Creek	12 Oct. 1989	91
r	Deena River	10 Oct. 1989	82
s	Pallant Creek	9 Oct. 1988	100
t	Lagoon Creek	mid-Oct. 1989	83
u	Salmon River	20 Oct. 1989	57
v	Sedgewick Creek	mid-Oct. 1989	74
w	Bag Harbor Creek	mid-Oct. 1989	89
x	Surprise Creek	mid-Oct. 1989	85
Area 3Z: Portland and Observatory Inlets – Nass River			
y	Kshwan River	13 Sept. 1988	88
z	Kitsault River	11 Aug. 1988	95
AA	Stagoo Creek	11 Aug. 1988	75
		18 Sept. 1989	53
BB	Khutzeymateen River	13 Sept. 1988	94
CC	Toon River	12 Sept. 1988	98
Area 4: Skeena River area			
DD	Ecstall River	12 Sept. 1988	99
Area 6			
EE	Kitimat River	6 Aug. 1988	92
		8 Aug. 1989	100
Area 7			
FF	Mussel River	27 Sept. 1989	31
GG	Neekas Creek	26 Sept. 1989	54
Area 8: Bella Coola River			
HH	Klownik Creek	31 Aug. 1989	100
Area 10			
II	Nekite Channel	15 Sept. 1989	100
JJ	Nekite River	30 Sept. 1989	97

We collected and analyzed samples from chum salmon throughout southeast Alaska and northern British Columbia to expand basic knowledge of their genetic population structure. Understanding the genetic variation may be useful to identify stocks in mixed-stock fisheries, to evaluate hatchery and wild stock interactions, and to protect wild stock genetic diversity. The present population structure may also provide insight into the postglacial dispersion of chum salmon in southeast Alaska and northern British Columbia.

Methods and Materials

Tissue samples were collected from adult chum salmon in 61 spawning locations in southeast Alaska and northern British Columbia between 1986 and 1990 (Fig. 1, Table 1). Several locations were sampled in more than one year to examine year-to-year differences. Muscle, heart, liver, and eye

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TABLE 2. Protein coding loci (Shaklee et al. 1990) for enzymes resolved in this study and the tissues and buffers in which they were resolved. Peptidase loci are also designated according to their substrate specificity. L, liver; H, heart; M, muscle; E, eye.

Enzyme	EC No.	Locus	Tissue (buffer[a])
Aconitate hydratase	4.2.1.3	*mAH-1,2**	H and L (B)
		*mAH-3**	H and L (B)
		*sAH**	L (B)
Alanine aminotransferase	2.6.1.2	*ALAT**[b,c]	M (H)
Aspartate aminotransferase	2.6.1.1	*mAAT-1**[b,c]	M (A), H (B)
		*sAAT-1,2**[b,c]	M (E), H (D)
		*sAAT-3**[b,c]	E (G)
Creatine kinase	2.7.3.2	*CK-A1**[c]	M (G)
		*CK-A2**[c]	M (G)
		*CK-B**[b,c]	E (J)
		*CK-C1**	E (J)
		*CK-C2**	E (J)
Esterase-D	3.1.-.-	*ESTD-1**[b,c]	M and H (H)
Fumarate hydratase	4.2.1.2	*FH**[b,c]	M (E), E (F)
Formaldehyde dehydrogenase (glutathione)	1.2.1.1	*FDHG**[c]	H and L (B)
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-A**[b,c]	M and H (G)
		*GPI-B1,2**[b]	M and H (G)
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-1**[c]	M (I), H (D)
		*G3PDH-2**[b,c]	H (D)
		*G3PDH-3**[b,c]	H (D)
L-Iditol dehydrogenase	1.1.1.14	*IDDH-1**[c]	H (G)
		*IDDH-2**[b,c]	L (G)
Isocitrate dehydrogenase ($NADP^+$)	1.1.1.42	*mIDHP-1**[b,c]	M (A)
		*mIDHP-2**[c]	M (A)
		*sIDHP-2**	L (B)
L-Lactate dehydrogenase	1.1.1.27	*LDH-A1**[b,c]	M (G)
		*LDH-A2**[c]	M (G)
		*LDH-B1**[c]	M, H, and E (G)
		*LDH-B2**[b,c]	M, H, L, and E (G)
		*LDH-C**[b,c]	E (G)
Malate dehydrogenase	1.1.1.37	*sMDH-A1**[b,c]	L (E), H (D)
		*sMDH-A2**[b,c]	H (D)
		*sMDH-B1,2**[b,c]	H (D), M and L (E)
Malic enzyme ($NADP^+$)	1.1.1.40	*mMEP-2**[b,c]	M (I)
		*sMEP-1**[b,c]	M (I)
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**[b,c]	H (C, H)
α-Mannosidase	3.2.1.24	*αMAN**[c]	H (I)
Peptidase	3.4.-.-		
Glycyl-leucine activity		*PEPA** (*GL*)[c]	H (G)
Leucyl-glycyl-glycine activity		*PEPB-1** (*LGG*)[b,c]	E (F, J)
Phosphoglucomutase	5.4.2.2	*PGM-1**[b,c]	H (D)
		*PGM-2**[b,c]	H (D), M (H)
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**[b,c]	M (A), L (B)
Triose-phosphate isomerase	5.3.1.1	*TPI-1**[b,c]	E (G), H (J)
		*TPI-2**[c]	E (G), H (J)
		*TPI-3**[b,c]	E (G), H (J)
		*TPI-4**[b,c]	E (G), H (J)

[a]A and B, CAME7.2 and CAME7.4, respectively (Aebersold et al. 1987); C, D, E, and F, modified Clayton and Tretiak (1972) to pH 7, 6.5, 6.1, and 5.75, respectively; G, R (Ridgway et al. 1970); H, MF (Markert and Faulhaber 1965); I, TC4 (buffer *a* of Schaal and Anderson 1974); J, TG (0.04 M Tris, 0.12 M glycine, equal concentration for gel and electrode).
[b]Locus included in principal component and multiple analysis of variance analyses.
[c]Locus included in gene diversity analysis and construction of neighbor-joining tree.

tissues from approximately 100 fish per location were stored on packs of frozen gel refrigerant and frozen at −20°C within hours of collection, then shipped to the Auke Bay Laboratory and stored as soon as possible at −80°C. Protein electrophoresis was conducted as described by Aebersold et al. (1987). Specific enzymes were stained according to Harris and Hopkinson (1976) or Aebersold et al. (1987). Loci for which data were obtained, the tissues in which they were expressed, and the buffer systems with which they were resolved are listed in Table 2.

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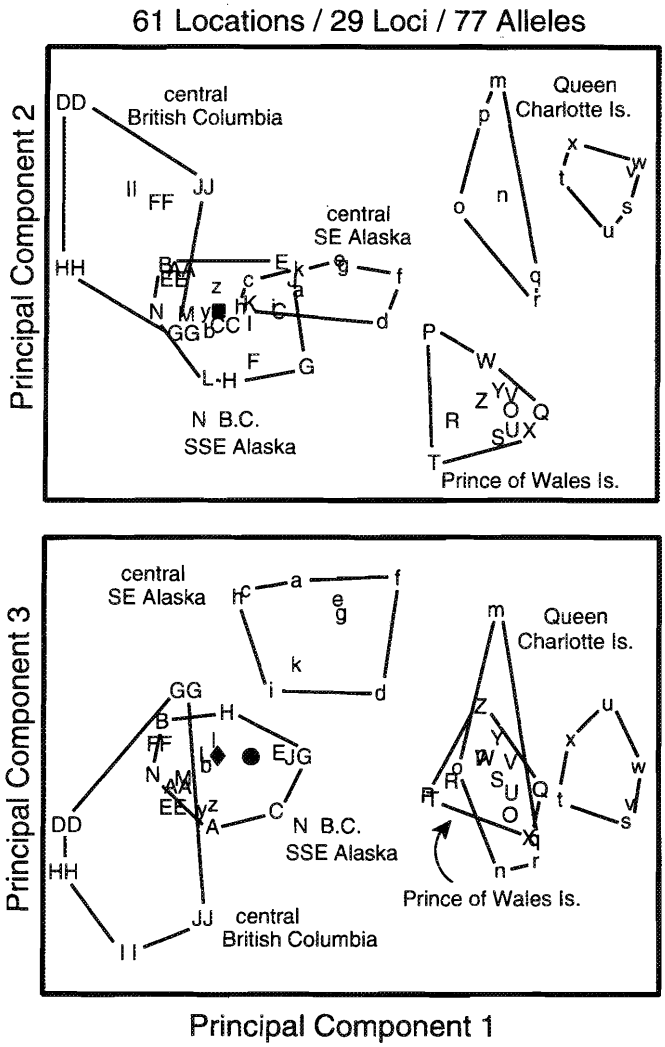

FIG. 2. Principal component analysis of southeast Alaska and northern British Columbia chum salmon for allelic frequencies of 29 loci (see Table 2). Letters correspond to location names in Table 1 and Figs. 1 and 3. N BC, = northern British Columbia; SSE Alaska, southern southeast Alaska. Letters that are indistinguishable as a result of overlap are represented by symbols: ■, A, D, I, DD; ◆, D, BB, CC; ●, F, I, K.

Departure from Hardy–Weinberg expectations was examined with χ^2 goodness-of-fit tests. Because Pearson's goodness-of-fit test is not asymptotic to the χ^2 distribution at low expected frequencies, a Monte Carlo resampling program was used to generate distributions of X^2 statistics for each test (A.J. Gharrett, unpublished data).

Hardy–Weinberg expectations were not tested in two situations: (*i*) locus *PGM-1** and (*ii*) isoloci. *PGM-1** has a null allele (nonstaining); only four of the possible six phenotypes were detectable for the three alleles we observed. Therefore, conformance to Hardy–Weinberg frequencies was not tested because genotypes could not be inferred. Other statistical tests using data from this locus used the observed phenotypic frequencies; however, assumed genotypic frequencies were used to calculate genetic distance and gene diversity. Hardy–Weinberg expectations were also not tested for comigrating, duplicated loci (isoloci) (Allendorf and Thorgaard 1984). Variation at isoloci was assigned to the loci based on maximum-likelihood methods (Waples 1988). Generally, both loci were assigned the variation when an isolocus was highly variable (*sAAT-1,2**); for isoloci with low variability, only one locus was assigned the variation, and the other was treated as monomorphic (*sMDH-B1,2**, *GPI-B1,2**, *mAH-1,2**).

Homogeneity of samples among years within locations was tested with log-likelihood ratio analysis (*G*-tests) (Sokal and Rohlf 1981). Homogeneity among locations and groups of locations was tested after initial descriptive analyses had been made. Because the *G*-statistic is not necessarily asymptotic to the χ^2 distribution when low-frequency alleles are involved, we generated a distribution of *G*-statistics for each test, using a Monte Carlo process. The *G*-statistic distributions were made by reconstructing each set of allele frequencies for a locus by randomly drawing from the weighted average of the allele frequencies (with replacement) the number of alleles originally observed in each collection and computing a *G*-statistic. The process was repeated 2000 times to generate a distribution. The proportion of *G*-statistics generated by the Monte Carlo process that exceeded the observed *G*-statistic was inferred as the probability of the test.

Relationships among collections were examined using two descriptive methods: principal component analysis (SAS Institute Inc. 1988) and construction of an unrooted tree using genetic distance. Principal component analysis was computed with the arc sine – square root transformed frequencies of $N - 1$ alleles. Alleles expressed in fewer than five fish were combined with the allele that had the most similar mobility. A neighbor-joining tree (Saitou and Nei 1987) was constructed with the chord distances (Cavalli-Sforza and Edwards 1967) between each pair of populations.

Multivariate analysis of variance (MANOVA) of arc sine – square root transformed allelic frequencies was used to examine the significance of the geographic structure of the populations sampled. Significance was inferred using Wilks' λ. Alleles expressed in fewer than five fish were combined with the allele that had the most similar mobility. Concern that low levels of variation at some loci might produce spurious results led us to determine significance levels by using a Monte Carlo resampling program to generate a distribution of *F*-statistics as described for the distribution of *G*-statistics (A.J. Gharrett, unpublished data). The proportion of *F*-statistics generated by the resampling process that exceeded the observed *F*-statistic generally was similar to the probability obtained from the *F*-distribution.

Genetic diversity was partitioned into components attributable to the average amount of variation at a collection site (H_S/H_T), differences among collections within a region [$G_{SR} = (H_R - H_S)/H_T$], and differences among regions [$G_{RT} = (H_T - H_R)/H_T$] (Chakraborty and Leimar 1987). H_S is the average expected heterozygosity of each sample site, H_R is the average expected heterozygosity within each region, and H_T is the overall average expected heterozygosity. In this analysis, average allelic frequencies were calculated from unweighted averages of the collections.

Results

Forty-six loci were resolved from 21 enzyme-specific stains. Of these, 42 were variable (including four isoloci), and 4 loci were monomorphic (*αMAN**, *mIDHP-2**, *LDH-B1**, and *IDDH-1**). Allelic frequencies are listed in Appendix 1.

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TABLE 3. Relative rank of the 12 most important loci with common allele frequencies <0.95 in the first three factors of the principal component analysis. *P* values are also included for the MANOVA and log-likelihood ratio (*G*-test) analyses.

Locus	PC1	PC2	PC3	MANOVA	*G*-test
*sAAT-3**	1	11	10	3×10^{-11}	$<10^{-6}$
*mIDHP-1**	2	9	6	2×10^{-11}	$<10^{-6}$
*mAAT-1**	3	12	9	5×10^{-10}	$<10^{-6}$
*PGM-1**	4	8	12	4×10^{-7}	$<10^{-6}$
*ESTD-1**	5	3	11	3×10^{-10}	$<10^{-6}$
*sMDH-A1**	6	6	8	8×10^{-9}	$<10^{-6}$
*G3PDH-2**	10	1	7	4×10^{-5}	$<10^{-6}$
*sAAT-1,2**	12	2	1	1×10^{-6}	$<10^{-6}$
*PEPB-1**	7	4	5	1×10^{-12}	$<10^{-6}$
*MPI**	11	5	2	6×10^{-4}	$<10^{-6}$
*mMEP-2**	9	7	3	2×10^{-6}	$<10^{-6}$
*FH**	8	10	4	1×10^{-2}	$<10^{-6}$

Departure from Hardy–Weinberg expectations occurred in 34 of a possible 1406 tests, which is less than expected by chance alone at an $\alpha = 0.05$. These departures occurred in fewer than half the loci analyzed; 8 of the 34 significant values occurred at the *G3PDH-2** locus and were due to an excess of homozygotes. The remaining significant departures from Hardy–Weinberg equilibrium were spread among those loci in which departures occurred.

At 15 locations, samples were collected in more than 1 yr. Although tests at individual loci showed some heterogeneity (26 of 349 tests), after adjustment for multiple testing (Cooper 1968), they were not significant. The overall tests (over all loci) were significant for 3 of the 15 locations (Herman Creek, Old Tom Creek, and Cruz Cove); but after taking multiple testing into account, only Herman Creek was heterogeneous over years. Because the samples were of consistently good quality and were collected from the same location at the same time of year, we pooled the allelic frequencies of collections within a location, including the one with a significant overall *G*-statistic, for subsequent analyses.

We observed distinct clustering of collections with principal component analysis that corresponded to six geographic regions (Fig. 2). This analysis was based on 29 variable loci (see Table 2) common to all collections, with a total of 77 alleles. The first three principal components accounted for 21, 11, and 8% of the observed genetic variation, respectively. The first component was useful in separating the Queen Charlotte Islands and Prince of Wales Island collections from the other collections. Collections in the Queen Charlotte Islands region separated into two groups: one included all the collections from the east side of Moresby Island (the more southerly of the two largest Queen Charlotte Islands; collections *s–x*); the second group consisted of collections from the outer coast, the north end of Graham Island (the more northerly large island), and the channel between Moresby and Graham islands (collections *m–r*). The second principal component was useful in separating the Queen Charlotte Islands collections from the Prince of Wales Island collections, and the third component splits the central southeast Alaska collections from southern southeast Alaska and north-central British Columbia collections.

The principal component plots suggest some separation between southern southeast Alaska – northern British Columbia (Portland and Observatory Inlets) collections and the collections from north to central British Columbia (DD–JJ); however, the differences are less distinct than between the other groups because several collections overlap. The two northern southeast Alaska collections did not form a distinct group. The Lynn Brothers collection (*k*) clustered with the central southeast Alaska collections, and the collection from Herman Creek (*l*), a Chilkat River tributary, clustered with southern southeast Alaska – northern British Columbia collections. The most variable loci, with a common allele frequency <0.95, useful in distinguishing geographic regional differences, are listed in Table 3. Some of the less common alleles, from loci with more than two alleles, were also important contributors (*sMDH-B1,2*72*, *sMDH-B1,2*50*, *sMDH-B1,2*129*; *MPI*e*[1]; *PEPB-1*b*, *PEPB-1*c*, *PEPB-1*d*, *PEPB-1*e*[2]; *GPI-A*95*, *GPI-A*105*).

Genetic distances used to construct a neighbor-joining tree were calculated from 40 loci (see Table 2), including invariant loci, that were common to all collections. The unrooted tree revealed virtually identical geographic groupings of the collections (Fig. 3). The one exception, the Port Real Marina collection (X), clustered with a Queen Charlotte Islands branch.

We grouped the collections for MANOVA based on these descriptive analyses. Testing for geographic structure used the six geographical regions as a fixed effect on the transformed allelic frequencies for a total of 77 alleles at 29 loci (see Table 2). The test was highly significant (Wilks' $\lambda = 1 \times 10^{-8}$, $F_{240,45} = 7.2093$, $P = 4 \times 10^{-12}$). All but seven loci (*PGM-2**, *CK-B**, *IDDH-2**, *sMEP-1**, *GPI-B1,2**, *TPI-3**, and *TPI-4**) had significant univariate *F*-tests based on the bootstrap resampling analysis. Allelic frequency data for *sIDHP-2**, *mAH-3**, *mAH-1,2**, and *sAH** were unavailable for Mussel River, Nekite Channel, Nekite River, Klownik Creek, Kitimat River, Ecstall River, Pallant Creek, Tombstone River, Marten River, Klahini River, Traitor's Creek, Eulachon Creek, Tokeen Creek, Elena Creek, Eliza Creek, and Gambier Creek. When these collections were removed from the analysis, the univariate *F*-statistics and *G*-tests from the log-likelihood analysis were also significant for *sIDHP-2**, *mAH-3**, and *mAH-1,2**.

The hierarchical log-likelihood ratio analysis corroborated the MANOVA results (approximate *F*-statistic = 11.325, 235 df in the numerator, 2585 df in the denominator, $P < 1 \times 10^{-6}$), where the *F*-statistic is approximated by $(G_{between}/df_{between})/(G_{within}/df_{within})$ (Appendix 2). We also found significant heterogeneity within every region, except the collections from the eastern side of Moresby Island (collections *s–x*). This suggests that additional genetic structure is present within the regional areas.

For the gene diversity analysis, we used the six geographic regions observed in the principal component analysis and neighbor-joining tree to estimate the proportion of variation attributable to three levels of hierarchy: within collections (H_S/H_T), among collections within regions (G_{SR}), and among regions (G_{RT}). Most of the genetic diversity (97% on average) was found within sampling locations; the

[1]Two buffers are required to resolve this locus; the *e* allele has mobilities 86 and 94 on CA7 and MF gels, respectively.

[2]Two buffers are required to resolve this locus; the mobilities for the *a*, *b*, *c*, *d*, and *e* alleles are **–100* and **100*, **–126* and **100*, **–127* and **59*, **–146* and **59*, and **–72* and **110* at CA5.75 and TG or R, respectively.

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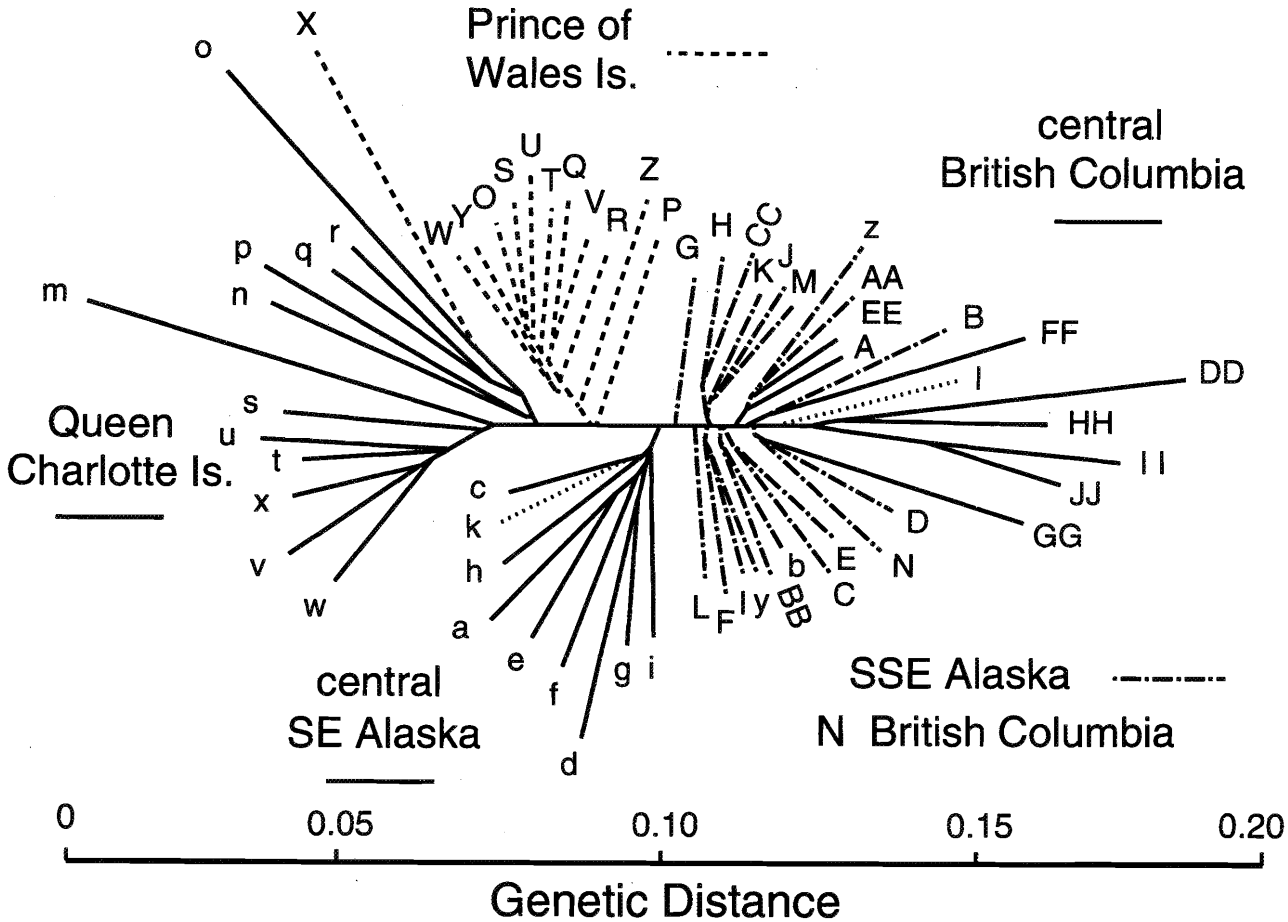

FIG. 3. Neighbor-joining tree (Saitou and Nei 1987) using genetic distances (Cavalli-Sforza and Edwards 1967) estimated from allelic frequencies of 40 loci (see Table 2). Letters correspond to location names in Table 1 and Figures 1 and 2. Genetic distances for populations "*k*" and "*l*" are indicated as (---) in the central southeast Alaska and central British Columbia population groups, respectively.

remaining variability was found almost equally within regions (1.3%) and among regions (1.4%).

Discussion

We observed significant allelic frequency differences both within and among regions; however, variation among regions was significantly greater. Data for almost half of the most important loci useful in distinguishing geographic regions in this study have not been previously reported (Okazaki 1982; Beacham et al. 1987). All but one location (Herman Creek) sampled in more than 1 yr had no significant year-to-year allelic frequency differences, indicating substantial stability of genetic structure within locations. Heterogeneity in Herman Creek samples suggests that subpopulation structure may exist in this location, a small tributary of the Chilkat River.

We compared allele frequencies at six loci (*sIDHP-2**, *mIDHP-1**, *mMEP-2**, *PGDH**, *G3PDH-2**, and *PEPB-1**) with those previously reported by Beacham et al. (1987) for 19 locations in northern British Columbia common to both studies. Of a possible 108 *G*-tests, 11 were significant. *PEPB-1** was the only locus that differed consistently among data sets; 4 of the 11 significant comparisons were due to this locus, which was more variable in our data than in Beacham et al. (1987). On closer examination, the two data sets were more similar than the initial analysis indicated. Beacham et al. (1987) had data for more than 1 yr for many locations, and we found that our data resembled theirs for at least 1 yr in 7 of the 11 significant tests. Thus, some of the differences may have been due as much to differences among years within the Beacham et al. (1987) study as to differences between their and our data sets.

Our analysis indicated the existence of six regional groups: Prince of Wales Island area, central southeast Alaska, southern southeast Alaska – northern British Columbia, north-central British Columbia, and two groups in the Queen Charlotte Islands area. Allele frequencies of mainland populations differed from those of the island populations; perhaps the mainland was colonized by fish moving north or south, rather than east from the two island groups. The Queen Charlotte Islands and Prince of Wales Island groups were clearly different from the other populations.

The Queen Charlotte Islands area had two distinct groups of populations. The greatest amount of heterogeneity observed within a region occurred in the northern and western Queen Charlotte Islands. Recent geologic work in the Queen Charlotte Islands has revealed that parts of this area were almost certainly ice free during the height of the last glaciation (Warner et al. 1982). Perhaps several chum salmon populations survived here, and due to isolation over time, have been subject to genetic drift longer than other populations examined in this

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study. The large amount of heterogeneity suggests a strong affinity for these populations to home to their natal streams. Alternatively, the differences reflect different local selection regimes or a combination of local selection and genetic drift.

A different situation exists on the eastern side of the Queen Charlotte Islands (collections *s–x*). These populations have similar allelic frequencies, which suggests that they may have descended from the same gene pool in more recent times. During the last glaciation, the shoreline here was lower because of lower ocean levels, and the configuration of the eastern side of Graham Island would have been greatly different from today. The present shallow passage between the northern half of the Queen Charlotte Islands and the mainland would have been land or ice, which would have blocked fish movement along the eastern side of the islands. The chum salmon on the inner coast probably survived as a smaller group, limited to the southeastern end of Moresby Island, and may have repopulated streams on the northeastern side of the Queen Charlotte Islands when sea levels rose as the glaciers retreated. Additional samples from the Queen Charlotte Islands, particularly the outer coast, may provide greater resolution of population structure relative to past glaciation and additional information about the size and nature of the refugium.

The Prince of Wales Island populations also exhibit heterogeneity, but less than the Queen Charlotte Islands populations. Information about past glaciation in this area is limited, but local areas of the outer coast of southeast Alaska may have been ice free during the late Wisconsin (Mann 1986; J. Baichtal, U.S. Forest Service, Ketchikan, AK 99901, personal communication). Perhaps part of the Prince of Wales Island area also served as a separate refuge during the height of this period. This could explain the large difference between these two regions. The Prince of Wales Island area was covered with ice more recently than the Queen Charlotte Islands area; repopulation of this region in more recent times would account for its greater homogeneity than the Queen Charlotte Islands area. Future study of northern southeast Alaska populations, particularly western Baranof Island, may provide further clues about the postglacial dispersal and possible refugia patterns along this coast.

Allozyme data are now available for much of the geographic distribution of chum salmon. Analysis of this baseline may reveal how postglacial dispersal resulted in the present distribution. Chum salmon probably survived in more than one unglaciated area (McPhail and Lindsey 1970), but only now is information available that allows us to infer patterns of colonization. It will be interesting to see whether the allele frequencies of chum salmon populations in southeast Alaska and northern British Columbia are more similar to those of populations from the Bering refuge (e.g., Yukon River, either via the marine environment around the Alaska Peninsula and Gulf of Alaska, or reverse flow of the Yukon River headwaters into southeast Alaska) or to those of populations from the Pacific refuge in Washington and Oregon.

The geographic basis for heterogeneity among regions is confounded in part by spawning-time differences. For example, the Prince of Wales Island and Queen Charlotte Islands chum salmon populations spawn in the fall, whereas the mainland populations of both southeast Alaska and northern British Columbia spawn mainly in the summer (Pacific Salmon Commission 1987). The summer runs are more protracted, and their timing may overlap slightly with that of the fall runs. Also, more southerly populations tend to spawn later.

Although the gene diversity values reported here cannot be compared directly with those of other studies because the loci included in different studies are not the same, the values for chum salmon populations from central southeast Alaska to central British Columbia are similar to those reported elsewhere (Okazaki 1982; Beacham et al. 1985, 1987; Wilmot et al. 1994).

National and international interest exists for using genetic information to estimate stock contributions in mixed-stock fisheries. Our genetic data can now be used in simulations to determine how accurately and precisely the allelic frequency differences can distinguish stock composition in a mixture. If our data can be used to estimate stock composition successfully, as has been done for chum fisheries in southern British Columbia and Washington (Beacham et al. 1987; S. Phelps, Washington Department of Fisheries, P.O. Box 43151, Olympia, WA 98504, personal communication; L. Hop Wo, Canada Department of Fisheries and Oceans, 3225 Stephenson Point Road, Nanaimo, BC, V9T 1K3, personal communication) it should be useful for management of mixed-stock chum salmon fisheries within Southeast Alaska and those fisheries near the southeast Alaska – British Columbia border.

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Appendix 1. Allozyme variation in collections of chum salmon from southeast Alaska and northern British Columbia. *N* = number of fish successfully screened at each locus. Alleles are designated by their mobility relative to the most common allele (**100*) and as described in Shaklee et al. (1990). Monomorphic loci include *αMAN**, *mIDHP-2**, *LDH-B1**, and *IDDH-1**. Rare variation is footnoted. Dashes (---) indicate no data.

		sAAT-1,2					mAAT-1				ALAT				ESTD-1					mIDHP-1[1]			LDH-A1[2]				LDH-B2			PEPB-1 (LGG)[3]					
Location		N	*100	*120	*80	*65	N	*-100	*-120	*-70	N	*100	*93	*105	N	*100	*91	*110	*80	N	*100	*60	N	*100	*50	*vslow	N	*100	*120	N	*a	*b	*c	*d	*e
District 101 - Behm Canal - Portland Canal - Boca de Quadra																																			
A. Fish	1986	100	0.84	0.16	0	0	100	0.71	0.23	0.07	59	0.75	0.25	0	100	0.95	0.05	0	0	100	0.87	0.13	99	0.96	0.04	0	100	1.00	0	60	0.77	0.03	0.07	0.12	0
	1987	50	0.87	0.13	0	0	50	0.68	0.26	0.06	50	0.81	0.18	0.01	50	0.96	0.04	0	0	50	0.86	0.14	50	0.97	0.03	0	50	1.00	0	10	0.80	0	0	0.20	0
early	1988	100	0.87	0.13	0	0	99	0.85	0.29	0.07	100	0.75	0.23	0.01	100	0.97	0.03	0	0	100	0.90	0.10	100	0.97	0.03	0	100	0.99	0.01	99	0.76	0.05	0.04	0.16	0
late	1988	52	0.90	0.10	0	0	52	0.62	0.34	0.05	49	0.84	0.16	0	52	0.94	0.06	0	0	52	0.85	0.15	52	0.97	0.03	0	52	1.00	0	52	0.78	0.04	0.04	0.14	0
B. Tombstone		96	0.89	0.11	0	0	98	0.66	0.30	0.05	96	0.83	0.17	0	97	0.94	0.06	0	0	97	0.90	0.10	98	0.98	0.02	0	98	1.00	0	56	0.79	0.03	0.04	0.14	0
C. Marton		104	0.87	0.13	0	0	104	0.75	0.18	0.07	63	0.80	0.19	0.01	104	0.93	0.07	0	0	105	0.95	0.05	105	0.98	0.02	0	105	1.00	0	65	0.81	0.03	0.03	0.13	0
D. Keta		101	0.91	0.09	0	0	98	0.74	0.20	0.06	101	0.79	0.20	0.01	101	0.93	0.07	0	0	101	0.90	0.10	101	0.99	0.01	0	101	0.99	0.01	58	0.75	0.03	0.05	0.16	0
E. Blossom		99	0.90	0.10	0	0	100	0.72	0.23	0.05	61	0.83	0.17	0	101	0.93	0.07	0.01	0	100	0.93	0.07	100	0.97	0.03	0	101	0.99	0.01	58	0.80	0.03	0.07	0.10	0
F. Wilson		102	0.86	0.14	0	0	102	0.68	0.27	0.05	62	0.82	0.15	0.02	103	0.93	0.07	0	0	102	0.90	0.10	102	0.97	0.03	0	103	0.995	0.005	63	0.80	0.07	0.03	0.10	0
G. Traitor's	1986	101	0.88	0.12	0	0	101	0.77	0.18	0.04	61	0.79	0.21	0	101	0.91	0.09	0	0	100	0.89	0.11	101	0.97	0.03	0	101	0.99	0.01	61	0.75	0.05	0.02	0.18	0
	1988	104	0.88	0.12	0	0	105	0.73	0.21	0.06	103	0.77	0.22	0.005	105	0.95	0.05	0	0	105	0.89	0.11	105	0.98	0.02	0	105	1.00	0	105	0.74	0.05	0.01	0.20	0
H. Carroll		100	0.88	0.12	0	0	99	0.62	0.36	0.03	59	0.69	0.31	0	100	0.94	0.06	0	0	100	0.92	0.08	100	0.95	0.05	0	100	0.99	0.01	60	0.82	0.03	0.04	0.12	0
I. Portage	1986	109	0.90	0.10	0	0	110	0.68	0.29	0.04	111	0.86	0.13	0.01	111	0.96	0.04	0	0	110	0.93	0.07	111	0.98	0.02	0	111	0.99	0.01	72	0.83	0.02	0.06	0.09	0
	1988	60	0.89	0.11	0	0	63	0.63	0.29	0.07	63	0.80	0.19	0.01	63	0.94	0.06	0	0	63	0.90	0.10	63	0.99	0.01	0	63	0.97	0.03	63	0.80	0.03	0.03	0.13	0
J. King	1986	100	0.86	0.14	0	0	100	0.73	0.22	0.05	60	0.75	0.24	0.01	100	0.95	0.05	0	0	99	0.92	0.08	100	0.95	0.05	0	100	1.00	0	60	0.73	0.04	0.04	0.18	0
	1988	52	0.89	0.11	0	0	52	0.74	0.21	0.05	47	0.78	0.20	0.02	52	0.93	0.07	0	0	52	0.94	0.06	52	0.96	0.04	0	52	1.00	0	52	0.87	0	0.02	0.12	0
K. Klahini		101	0.88	0.12	0	0	102	0.69	0.29	0.02	100	0.75	0.23	0.01	102	0.93	0.07	0	0	102	0.93	0.07	102	0.97	0.03	0	102	1.00	0	62	0.81	0.06	0.03	0.10	0
L. Eulachon		87	0.88	0.12	0	0	89	0.72	0.23	0.05	50	0.78	0.21	0.01	90	0.94	0.06	0	0	90	0.87	0.13	90	0.99	0.01	0	90	1.00	0	50	0.80	0.03	0.04	0.13	0
M. Grant		127	0.90	0.10	0	0	124	0.69	0.27	0.04	125	0.78	0.22	0	126	0.96	0.04	0	0	127	0.93	0.07	127	0.98	0.02	0	127	1.00	0	87	0.81	0.03	0.05	0.11	0
N. Herman		100	0.85	0.15	0	0	98	0.71	0.27	0.02	100	0.87	0.13	0	99	0.95	0.05	0.01	0	100	0.89	0.11	100	0.97	0.03	0	100	1.00	0	59	0.81	0.02	0.06	0.11	0
District 102 - Eastern Prince of Wales Island																																			
O. Kugel		104	0.85	0.15	0	0	104	0.86	0.11	0.03	102	0.88	0.12	0	104	0.86	0.14	0	0	103	0.97	0.03	103	0.98	0.02	0	104	0.98	0.02	64	0.74	0.03	0.02	0.20	0
P. Aiken		100	0.87	0.13	0	0	100	0.91	0.09	0.01	99	0.85	0.15	0	100	0.93	0.07	0	0	100	0.93	0.07	100	0.99	0.01	0	100	1.00	0	59	0.77	0.02	0.03	0.16	0
Q. Disappearance	1986	100	0.85	0.15	0	0	100	0.85	0.11	0.03	60	0.83	0.17	0	100	0.87	0.13	0	0	99	0.99	0.01	99	0.94	0.06	0	100	0.99	0.01	59	0.76	0.03	0.03	0.17	0
	1988	98	0.86	0.14	0	0	100	0.85	0.13	0.02	98	0.80	0.20	0	100	0.82	0.18	0	0	100	0.97	0.03	98	0.97	0.03	0	100	0.99	0.01	97	0.76	0.03	0.05	0.16	0
R. Lagoon		101	0.89	0.11	0	0	102	0.83	0.13	0.04	58	0.78	0.22	0	102	0.87	0.13	0	0	95	0.96	0.04	98	0.96	0.04	0	102	0.99	0.01	62	0.76	0.03	0.03	0.18	0
S. Old Tom	1986	100	0.86	0.14	0.003	0	100	0.89	0.07	0.05	97	0.80	0.20	0	100	0.78	0.22	0	0	100	0.96	0.04	100	1.00	0	0	100	0.99	0.01	59	0.72	0.06	0.04	0.18	0
	1988	52	0.90	0.10	0	0	50	0.88	0.10	0.02	47	0.81	0.19	0	52	0.90	0.10	0	0	52	1.00	0	51	0.98	0.02	0	52	0.97	0.03	52	0.73	0.09	0.05	0.13	0
T. Cabin		100	0.85	0.15	0	0	103	0.88	0.08	0.04	62	0.86	0.14	0	103	0.86	0.14	0	0	103	0.93	0.07	103	0.96	0.04	0	103	0.98	0.02	62	0.77	0.06	0.03	0.14	0
U. Karta		100	0.87	0.13	0	0	99	0.85	0.06	0.09	97	0.75	0.25	0	100	0.87	0.13	0	0	99	0.97	0.03	100	0.98	0.02	0	100	0.99	0.01	60	0.74	0.04	0.02	0.20	0
District 103 - Western Prince of Wales Island																																			
V. Coco Harbor		99	0.87	0.13	0	0	100	0.82	0.15	0.03	100	0.84	0.17	0	100	0.87	0.13	0	0	100	0.95	0.05	100	0.97	0.03	0	100	0.99	0.01	59	0.78	0.03	0.03	0.17	0
W. Breezy Bay	1986	100	0.90	0.10	0	0	100	0.85	0.13	0.02	80	0.87	0.13	0	100	0.90	0.10	0	0.01	100	0.97	0.03	100	0.90	0.10	0	100	0.97	0.03	60	0.74	0	0.03	0.23	0
	1987	100	0.86	0.14	0	0	100	0.89	0.11	0.01	89	0.82	0.18	0	99	0.90	0.09	0	0.01	100	0.97	0.03	100	0.95	0.05	0	100	0.99	0.01	59	0.76	0.05	0.01	0.18	0
	1988	54	0.83	0.17	0	0	54	0.88	0.10	0.02	84	0.91	0.09	0	54	0.89	0.10	0	0.01	54	0.94	0.06	54	0.96	0.04	0	54	0.96	0.04	54	0.77	0.01	0.06	0.16	0
X. Port Real Marina	1986	100	0.86	0.14	0	0	100	0.87	0.12	0.01	80	0.85	0.15	0	100	0.83	0.17	0	0	100	0.91	0.09	100	0.97	0.03	0	100	0.98	0.02	60	0.72	0.07	0.07	0.14	0
	1988	48	0.83	0.17	0	0	48	0.84	0.16	0	48	0.78	0.22	0	48	0.85	0.15	0	0	47	0.91	0.09	48	0.98	0.02	0	48	0.98	0.02	48	0.75	0.05	0.04	0.16	0
Y. Cruz Cove	1986	84	0.85	0.15	0	0	84	0.89	0.10	0.02	---	---	---	---	84	0.86	0.14	0	0	83	0.95	0.05	83	0.98	0.02	0	84	0.99	0.01	44	0.67	0.03	0.11	0.18	0
	1987	56	0.92	0.08	0	0	56	0.80	0.19	0.01	54	0.79	0.21	0	56	0.80	0.20	0	0	56	0.96	0.04	56	0.96	0.04	0	56	0.95	0.05	16	0.84	0.03	0.03	0.09	0
	1988	53	0.89	0.11	0	0	53	0.88	0.09	0.03	52	0.79	0.16	0.03	53	0.77	0.23	0	0	53	0.95	0.05	53	0.98	0.02	0	53	0.95	0.05	53	0.77	0.02	0.05	0.16	0
Z. Tokeen		101	0.89	0.11	0	0	101	0.74	0.23	0.03	59	0.84	0.16	0	100	0.78	0.22	0	0	101	0.98	0.02	100	0.96	0.04	0	101	0.99	0.01	59	0.78	0.06	0	0.16	0
District 105 - Western Sumner Strait																																			
a. Irish		97	0.92	0.08	0	0	98	0.78	0.18	0.04	98	0.90	0.10	0	98	0.97	0.03	0	0	98	0.94	0.06	98	0.97	0.03	0	98	0.99	0.01	58	0.85	0.04	0	0.10	0
District 107 - Ernest Sound - Bradfield Canal																																			
b. Harding		94	0.88	0.12	0	0	94	0.65	0.28	0.07	91	0.81	0.19	0.01	95	0.93	0.07	0	0	94	0.93	0.07	94	0.97	0.03	0	95	0.99	0.01	55	0.76	0.02	0.08	0.14	0
District 108 - Stikine River																																			
c. North Arm		81	0.92	0.08	0	0	80	0.66	0.28	0.06	81	0.80	0.20	0	81	0.96	0.04	0	0	81	0.92	0.08	81	0.96	0.04	0	81	1.00	0	41	0.80	0.02	0.04	0.13	0
District 109 - Southern Chatham Strait - Western Frederick Sound																																			
d. Lover's Cove	1987	100	0.90	0.06	0	0.04	100	0.78	0.21	0.01	100	0.81	0.19	0	100	0.93	0.07	0	0	100	0.95	0.05	100	0.97	0.03	0	100	0.99	0.01	60	0.87	0.03	0.06	0.04	0
	1990	31	0.91	0.06	0	0.02	31	0.76	0.24	0	27	0.87	0.13	0	31	0.92	0.06	0	0	30	0.98	0.02	31	0.95	0.06	0	31	1.00	0	30	0.87	0.07	0.05	0.02	0
e. Elena Bay		61	0.95	0.05	0	0	61	0.77	0.20	0.02	61	0.93	0.07	0.01	61	0.95	0.05	0	0	61	0.93	0.07	56	0.94	0.06	0	61	1.00	0	61	0.82	0.03	0.04	0.11	0
f. Eliza Harbor		61	0.98	0.02	0	0	61	0.74	0.20	0.07	60	0.82	0.18	0	61	0.89	0.11	0	0	61	0.93	0.07	61	0.95	0.05	0	61	0.99	0.01	61	0.76	0.05	0.05	0.14	0
District 110 - Eastern Frederick Sound																																			
g. Donkey	1986	60	0.91	0.07	0	0.02	99	0.70	0.27	0.04	99	0.83	0.17	0	100	0.97	0.03	0	0	100	0.95	0.05	98	0.94	0.06	0	100	0.99	0.01	60	0.82	0.01	0.03	0.14	0
	1990	61	0.91	0.08	0	0.01	59	0.80	0.17	0.03	48	0.80	0.20	0	61	0.98	0.03	0	0.01	60	0.93	0.07	61	0.96	0.04	0	61	0.97	0.03	61	0.81	0.02	0.03	0.13	0
h. Pybus Bay		65	0.92	0.08	0.004	0	65	0.73	0.25	0.02	65	0.82	0.18	0	65	0.95	0.05	0	0	65	0.96	0.04	65	0.96	0.04	0	65	1.00	0	65	0.86	0.01	0.03	0.10	0
i. Gambier Bay	1989	27	0.90	0.10	0	0	27	0.63	0.31	0.06	24	0.87	0.13	0	27	0.94	0.06	0	0	27	0.96	0.04	27	0.98	0.02	0	27	1.00	0	27	0.80	0.02	0.02	0.17	0
	1990	40	0.91	0.09	0	0	39	0.68	0.28	0.04	29	0.84	0.16	0	40	0.95	0.04	0.01	0	40	0.90	0.10	40	0.97	0.03	0	40	1.00	0	38	0.79	0.09	0.04	0.08	0
District 115 - Lynn Canal																																			
k. Lynn Brothers		50	0.90	0.09	0.01	0	50	0.72	0.24	0.04	49	0.84	0.16	0	50	0.96	0.04	0	0	50	0.92	0.08	50	0.95	0.05	0	50	1.00	0	49	0.80	0.02	0.03	0.15	0
l. Herman	1987	99	0.91	0.09	0	0	99	0.62	0.32	0.06	99	0.87	0.13	0	99	0.96	0.04	0	0	100	0.89	0.11	100	0.95	0.05	0	100	1.00	0	60	0.70	0.08	0.05	0.17	0
	1990	59	0.89	0.11	0	0	59	0.63	0.29	0.08	59	0.89	0.11	0	59	0.92	0.08	0	0	59	0.94	0.06	59	0.98	0.02	0	58	1.00	0	58	0.85	0.02	0.01	0.12	0
Area 1 - Northern Queen Charlotte Islands																																			
m. Awun		75	0.97	0.03	0	0	75	0.95	0.05	0	75	0.69	0.31	0	75	0.94	0.06	0	0	75	1.00	0	75	0.99	0.01	0	75	0.89	0.11	74	0.68	0.04	0	0.28	0
Area 2 - Western Queen Charlotte Islands																																			
n. Mace		99	0.88	0.12	0	0	100	0.65	0.35	0	97	0.93	0.07	0	100	0.95	0.05	0	0	99	0.97	0.03	99	0.97	0.03	0	100	0.98	0.02	100	0.70	0.01	0.01	0.28	0
o. Peel		75	0.90	0.10	0	0	75	0.76	0.24	0	75	0.78	0.21	0.01	75	0.95	0.05	0	0	75	0.97	0.03	75	0.92	0.08	0	75	0.97	0.03	75	0.60	0.04	0.07	0.29	0
p. Tasu		100	0.91	0.09	0	0	100	0.85	0.15	0	98	0.72	0.26	0.02	100	0.97	0.03	0	0	98	0.94	0.06	97	0.97	0.03	0	100	1.00	0	98	0.61	0.05	0.04	0.31	0
Area 2 - Eastern Queen Charlotte Islands																																			
q. Lagins		89	0.85	0.15	0	0	91	0.80	0.19	0.01	91	0.81	0.18	0.01	91	0.88	0.12	0	0	91	0.98	0.02	91	0.98	0.02	0	91	0.93	0.07	91	0.58	0.03	0.06	0.32	0
r. Deena		82	0.84	0.16	0	0	82	0.81	0.19	0	81	0.88	0.12	0	82	0.86	0.14	0	0	82	0.96	0.04	82	0.96	0.04	0	82	0.88	0.12	82	0.73	0.02	0.01	0.24	0
s. Pallant		100	0.91	0.09	0	0	100	0.83	0.15	0.01	100	0.85	0.15	0.01	100	0.85	0.15	0	0	100	0.97	0.03	100	0.95	0.05	0	100	0.94	0.07	100	0.71	0.06	0.01	0.23	0
t. Lagoon		81	0.92	0.08	0	0	83	0.83	0.17	0	83	0.85	0.14	0.01	83	0.95	0.05	0	0	83	0.98	0.02	83	0.94	0.05	0.01	83	0.95	0.06	82	0.66	0.07	0.01	0.27	0
u. Salmon		57	0.94	0.06	0	0	57	0.89	0.10	0.01	57	0.82	0.14	0.04	57	0.91	0.09	0	0	57	1.00	0	57	0.94	0.05	0.01	57	0.96	0.04	56	0.70	0.04	0	0.26	0
v. Sedgewick		74	0.91	0.09	0	0	74	0.86	0.14	0	74	0.86	0.11	0.02	74	0.91	0.09	0	0	74	0.96	0.02	74	0.92	0.08	0	74	0.93	0.07	73	0.60	0.08	0	0.32	0
w. Bag Harbor		89	0.92	0.08	0	0	89	0.85	0.15	0	86	0.85	0.13	0.02	89	0.90	0.10	0	0	89	0.99	0.01	89	0.93	0.07	0	89	0.95	0.05	89	0.69	0.06	0.02	0.22	0.01
x. Surprise		84	0.94	0.06	0	0	85	0.83	0.17	0	84	0.85	0.14	0.01	85	0.94	0.06	0	0	85	0.99	0.01	85	0.95	0.05	0	85	0.96	0.04	85	0.64	0.06	0.01	0.29	0
Area 3Z - Portland - Observatory Inlets																																			
y. Kshwan		88	0.86	0.14	0	0	88	0.66	0.28	0.04	88	0.82	0.15	0.03	88	0.97	0.03	0	0	88	0.85	0.15	88	0.99	0.01	0	88	0.99	0.01	87	0.79	0.05	0.07	0.09	0
z. Kitsault		95	0.84	0.16	0	0	95	0.58	0.33	0.09	95	0.85	0.14	0.01	95	0.94	0.06	0	0	95	0.88	0.12	95	0.95	0.05	0	95	0.98	0.02	95	0.77	0.02	0.04	0.17	0
AA. Stagoo	1988	75	0.83	0.17	0	0	75	0.63	0.32	0.05	75	0.80	0.19	0.01	75	0.98	0.02	0	0	75	0.87	0.13	75	0.99	0.01	0	75	1.00	0	73	0.79	0.05	0.05	0.10	0
	1989	51	0.90	0.10	0	0	53	0.68	0.24	0.08	53	0.84	0.15	0.01	53	0.95	0.05	0	0	53	0.89	0.11	53	0.94	0.06	0	53	1.00	0	53	0.79	0.07	0.04	0.10	0
BB. Khutzeymateen		94	0.89	0.11	0	0	94	0.85	0.28	0.07	94	0.79	0.21	0.01	94	0.96	0.04	0	0	94	0.89	0.11	94	0.97	0.03	0	94	1.00	0	93	0.73	0.01	0.08	0.18	0
CC. Toon		97	0.87	0.13	0	0	98	0.64	0.30	0.06	98	0.71	0.29	0.01	98	0.96	0.04	0	0	98	0.90	0.10	98	0.97	0.03	0	98	0.99	0.01	98	0.78	0.02	0.06	0.15	0
Area 4 - Skeena River																																			
DD. Ecstall		99	0.93	0.07	0	0	99	0.41	0.42	0.17	99	0.90	0.10	0.005	99	0.99	0.01	0	0	99	0.97	0.03	99	0.99	0.01	0	99	1.00	0	98	0.74	0.08	0.06	0.12	0
Area 6																																			
EE. Kitimat	1988	91	0.85	0.15	0	0	92	0.66	0.27	0.08	92	0.82	0.16	0	92	0.97	0.03	0	0	92	0.86	0.14	92	0.97	0.03	0	92	1.00	0	88	0.74	0.03	0.04	0.19	0
	1989	99	0.90	0.10	0	0	100	0.69	0.25	0.06	100	0.80	0.19	0.01	100	0.95	0.05	0	0	100	0.87	0.13	100	0.97	0.03	0	100	0.99	0.01	99	0.82	0.02	0.05	0.12	0
Area 7																																			
FF. Mussel		31	0.92	0.08	0	0	31	0.77	0.19	0.03	31	0.77	0.23	0	31	0.97	0.03	0	0	31	0.87	0.13	30	1.00	0	0	31	1.00	0	31	0.63	0.02	0.05	0.31	0
GG. Neekas		53	0.92	0.06	0.005	0	53	0.81	0.14	0.05	53	0.84	0.14	0.02	53	0.90	0.10	0	0	53	0.92	0.08	53	0.98	0.02	0	53	0.99	0.01	53	0.81	0.01	0.08	0.10	0
Area 8 - Bella Coola River					0																														
HH. Klownik		99	0.88	0.12	0	0	100	0.69	0.27	0.04	99	0.87	0.13	0	100	1.00	0	0	0	99	0.83	0.17	99	0.99	0.01	0	100	0.99	0.01	100	0.78	0.04	0.03	0.15	0
Area 10																																			
II. Nekite Channel		93	0.90	0.09	0.01	0	100	0.69	0.28	0.03	95	0.94	0.06	0	100	0.97	0.03	0	0	100	0.83	0.17	100	1.00	0	0	100	1.00	0	100	0.70	0.08	0.01	0.20	0.01
JJ. Nekite River		95	0.91	0.09	0	0	97	0.72	0.18	0.10	93	0.95	0.05	0	97	0.97	0.03	0	0	95	0.91	0.09	96	1.00	0	0	97	1.00	0	96	0.73	0.08	0.02	0.19	0.01

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Appendix 1. (*Continued*)

Location	sMDH-B1,2 N	*100	*50	*127	*72	*135	*129	mMEP-2 N	*100	*122	GPI-A N	*100	*95	*105	PGDH N	*100	*88	*110	G3PDH-1 N	*-100	*-110	*-76
District 101 - Behm Canal - Portland Canal - Boca de Quadra																						
A.	60	0.98	0.01	0	0.01	0	0	94	0.89	0.11	100	1.00	0	0	100	1.00	0	0	100	0.99	0.01	0
	50	0.96	0	0	0.04	0	0	49	0.78	0.22	50	1.00	0	0	50	1.00	0	0	50	1.00	0	0
	100	0.98	0	0	0.04	0	0	100	0.89	0.11	100	1.00	0	0	100	1.00	0	0	100	1.00	0	0
	52	1.00	0	0	0	0	0	49	0.88	0.12	52	1.00	0	0	52	1.00	0	0	52	1.00	0	0
B.	58	0.99	0	0	0.01	0	0	98	0.91	0.09	98	1.00	0	0	98	0.97	0.03	0.01	98	1.00	0	0
C.	65	0.96	0	0	0.02	0.01	0.01	105	0.87	0.13	105	0.995	0.005	0	105	0.99	0.01	0	105	1.00	0	0
D.	100	0.97	0.01	0	0.03	0	0	100	0.91	0.09	100	1.00	0	0	101	1.00	0	0	101	1.00	0	0
E.	101	0.97	0	0	0.02	0.01	0.01	101	0.90	0.10	101	1.00	0	0	101	0.98	0.02	0	101	1.00	0	0
F.	102	0.98	0	0	0.02	0	0	101	0.90	0.10	103	0.995	0.005	0	103	0.99	0.01	0	102	1.00	0	0
G.	61	0.99	0	0	0.01	0	0	100	0.89	0.11	101	1.00	0	0	101	1.00	0	0	101	1.00	0	0
	105	0.98	0	0	0.02	0	0	104	0.92	0.06	105	0.995	0.005	0	105	1.00	0	0	105	1.00	0	0
H.	60	0.98	0	0	0.02	0	0	98	0.92	0.08	100	0.99	0.01	0.01	100	0.99	0.01	0	99	1.00	0	0
I.	111	0.98	0	0.005	0.02	0	0	111	0.92	0.08	111	0.995	0.005	0	111	0.97	0.03	0	111	1.00	0	0
	63	0.98	0	0	0.02	0	0	63	0.90	0.10	63	1.00	0	0	63	0.98	0.02	0	63	1.00	0	0
J.	59	0.97	0.02	0	0.02	0	0	100	0.93	0.07	100	1.00	0	0	100	0.97	0.03	0	99	1.00	0	0
	52	0.97	0	0	0.03	0	0	52	0.92	0.08	52	1.00	0	0	52	0.95	0.05	0	52	1.00	0	0
K.	102	0.97	0.01	0	0.02	0	0	102	0.89	0.11	102	1.00	0	0	102	0.99	0.01	0	101	1.00	0	0
L.	50	1.00	0	0	0	0	0	90	0.92	0.08	90	0.98	0.01	0.01	90	0.99	0.01	0	90	1.00	0	0
M.	87	0.96	0.02	0	0.02	0	0	127	0.89	0.11	127	1.00	0	0	127	0.996	0.004	0	127	1.00	0	0
N.	99	0.96	0.01	0	0.03	0	0	99	0.85	0.15	100	1.00	0	0	100	0.99	0.01	0	99	1.00	0	0
District 102 - Eastern Prince of Wales Island																						
O.	64	0.94	0	0.01	0.05	0	0.01	102	0.97	0.03	104	0.97	0.01	0.01	104	0.995	0.005	0	103	1.00	0	0
P.	60	0.95	0	0	0.04	0	0.01	100	0.94	0.06	100	1.00	0	0	100	0.99	0.01	0	99	1.00	0	0
Q.	60	0.95	0	0.01	0.03	0	0.02	100	0.95	0.05	96	1.00	0	0	100	0.99	0.01	0	100	1.00	0	0
	100	0.93	0	0	0.06	0	0.01	99	0.93	0.07	98	0.99	0.01	0	100	0.99	0.01	0	100	1.00	0	0
R.	62	0.99	0	0	0.01	0	0	98	0.94	0.06	100	0.97	0.02	0.01	102	1.00	0	0	100	1.00	0	0
S.	59	0.96	0	0.01	0.03	0	0	100	0.95	0.05	100	0.97	0.03	0	100	0.99	0.01	0	100	1.00	0	0
	52	0.98	0	0	0.03	0	0.01	52	0.94	0.06	52	0.96	0	0.04	52	0.97	0.03	0	52	1.00	0	0
T.	62	0.99	0	0	0.01	0	0	103	0.95	0.05	103	0.96	0.01	0.01	103	1.00	0	0	103	1.00	0	0
U.	60	0.97	0	0	0.03	0	0	100	0.96	0.04	100	0.97	0.03	0	100	0.99	0.01	0	100	1.00	0	0
District 103 - Western Prince of Wales Island																						
V.	100	0.97	0	0	0.03	0	0.01	96	0.95	0.05	100	0.98	0.01	0.01	100	0.98	0.02	0	99	1.00	0	0
W.	60	0.94	0	0	0.06	0	0	96	0.91	0.09	100	0.99	0.01	0	100	0.99	0.01	0	100	1.00	0	0
	100	0.91	0	0	0.09	0	0	99	0.91	0.09	100	0.99	0.01	0.01	100	0.99	0.01	0	60	1.00	0	0
	54	0.90	0	0	0.10	0	0	54	0.93	0.07	53	0.99	0.01	0	54	1.00	0	0	54	1.00	0	0
X.	60	0.90	0	0	0.10	0	0	100	0.93	0.07	99	1.00	0	0	100	1.00	0	0	100	1.00	0	0
	48	0.96	0	0.01	0.04	0	0	48	0.94	0.06	45	0.97	0.02	0.01	48	1.00	0	0	48	1.00	0	0
Y.	44	0.90	0	0.01	0.09	0	0	83	0.95	0.05	80	0.99	0.01	0	84	0.98	0.02	0	84	1.00	0	0
	56	0.94	0	0.01	0.05	0	0	56	0.95	0.05	56	0.99	0	0.01	56	0.99	0.01	0	58	1.00	0	0
	53	0.91	0	0	0.09	0	0	52	0.87	0.13	47	1.00	0	0	53	0.99	0.01	0	53	1.00	0	0
Z.	60	0.94	0	0	0.08	0	0	99	0.98	0.02	97	0.99	0.01	0	101	0.99	0.01	0	101	1.00	0	0
District 105 - Western Sumner Strait																						
a.	98	0.97	0	0	0.03	0	0	98	0.91	0.09	98	0.99	0.01	0	58	0.95	0.05	0	98	1.00	0	0
District 107 - Ernest Sound - Bradfield Canal																						
b.	95	0.99	0	0	0.01	0	0	93	0.88	0.12	94	1.00	0	0	95	0.99	0.01	0	95	1.00	0	0
District 108 - Stikine River																						
c.	81	0.98	0	0	0.02	0	0	79	0.96	0.04	80	1.00	0	0	81	0.96	0.04	0	81	1.00	0	0
District 109 - Southern Chatham Strait - Western Frederick Sound																						
d.	100	0.97	0	0	0.03	0	0	99	0.97	0.03	100	1.00	0	0	100	0.97	0.01	0.02	100	1.00	0	0
	31	0.95	0	0	0.05	0	0	30	0.95	0.05	31	1.00	0	0	31	0.94	0.03	0.03	31	1.00	0	0
e.	61	0.95	0	0	0.05	0	0	55	0.94	0.06	60	1.00	0	0	61	0.97	0.03	0	61	1.00	0	0
f.	61	0.96	0	0	0.04	0	0	60	0.97	0.03	58	0.99	0.01	0	61	0.98	0.02	0	61	1.00	0	0
District 110 - Eastern Frederick Sound																						
g.	100	0.99	0	0	0.01	0	0	96	0.90	0.10	100	0.99	0	0.01	100	0.94	0.05	0.01	100	1.00	0	0
	61	0.93	0	0	0.07	0	0	61	0.95	0.05	40	1.00	0	0	61	0.97	0.03	0	61	1.00	0	0
h.	65	0.98	0.01	0	0.02	0	0	64	0.98	0.02	65	1.00	0	0	65	0.98	0.02	0	65	1.00	0	0
i.	27	0.96	0	0	0.04	0	0	24	0.94	0.06	27	1.00	0	0	27	1.00	0	0	27	1.00	0	0
	40	1.00	0	0	0	0	0	39	0.94	0.06	40	1.00	0	0	40	1.00	0	0	40	1.00	0	0
District 115 - Lynn Canal																						
k.	50	0.98	0	0	0.02	0	0	50	0.91	0.09	50	1.00	0	0	50	0.95	0.05	0	50	1.00	0	0
l.	100	0.97	0	0	0.03	0	0	100	0.92	0.08	100	0.99	0.01	0	100	0.99	0.01	0	89	1.00	0	0
	59	0.95	0	0	0.05	0	0	59	0.97	0.03	59	0.98	0.02	0	59	1.00	0	0	59	1.00	0	0
Area 1 - Northern Queen Charlotte Islands																						
m.	75	0.99	0	0	0.01	0	0.01	75	0.99	0.01	75	1.00	0	0	75	0.86	0.14	0	75	0.99	0	0.01
Area 2 - Western Queen Charlotte Islands																						
n.	100	0.86	0	0.01	0.12	0	0.01	99	0.82	0.18	99	1.00	0	0	99	0.98	0.02	0	99	1.00	0	0
o.	75	0.97	0	0	0.03	0	0	75	0.89	0.11	75	1.00	0	0	75	0.96	0.04	0	75	1.00	0	0
p.	100	0.95	0	0	0.05	0	0.01	98	0.81	0.19	99	1.00	0	0	100	0.91	0.09	0	98	1.00	0	0
Area 2 - Eastern Queen Charlotte Islands																						
q.	91	0.92	0	0	0.08	0	0	91	0.83	0.17	87	1.00	0	0	91	0.97	0.03	0	66	1.00	0	0
r.	82	0.95	0	0	0.04	0	0.01	82	0.89	0.11	82	1.00	0	0	82	0.99	0.01	0	82	1.00	0	0
s.	100	0.91	0	0	0.08	0	0.01	100	0.90	0.10	98	1.00	0	0	100	0.95	0.05	0	100	0.99	0	0.01
t.	83	0.90	0	0	0.09	0	0.01	83	0.91	0.09	82	1.00	0	0	83	0.99	0.01	0	83	1.00	0	0
u.	57	0.95	0	0	0.04	0	0.01	57	0.93	0.07	55	1.00	0	0	57	0.99	0.01	0	57	1.00	0	0
v.	74	0.93	0	0.01	0.05	0	0.01	74	0.91	0.09	74	1.00	0	0	74	0.98	0.02	0	74	1.00	0	0
w.	89	0.95	0	0	0.03	0	0.02	85	0.84	0.16	88	1.00	0	0	89	0.94	0.06	0	89	1.00	0	0
x.	85	0.96	0	0.01	0.02	0	0.01	85	0.89	0.11	85	1.00	0	0	85	0.96	0.04	0	85	1.00	0	0
Area 3Z - Portland - Observatory Inlets																						
y.	88	0.97	0	0	0.03	0	0	85	0.89	0.11	86	1.00	0	0	88	0.99	0.01	0	88	1.00	0	0
z.	95	0.95	0.01	0.01	0.04	0	0	95	0.85	0.15	92	1.00	0	0	95	0.99	0.01	0	95	1.00	0	0
AA.	75	0.94	0.01	0	0.05	0	0	75	0.83	0.17	75	1.00	0	0	75	0.99	0.01	0	75	0.99	0.01	0
	53	0.91	0.02	0	0.08	0	0	53	0.92	0.08	52	1.00	0	0	53	0.99	0.01	0	53	0.98	0.02	0
BB.	94	0.96	0.01	0	0.02	0.01	0	93	0.85	0.15	90	0.99	0	0.01	94	0.98	0.02	0	94	1.00	0	0
CC.	97	0.95	0	0	0.05	0	0	98	0.93	0.07	98	1.00	0	0	98	0.99	0.01	0	98	1.00	0	0
Area 4 - Skeena River																						
DD.	99	0.94	0.04	0	0.02	0	0	97	0.94	0.06	94	1.00	0	0	99	0.98	0.02	0	99	1.00	0	0
Area 6																						
EE.	92	0.98	0	0	0.02	0	0	90	0.87	0.13	19	1.00	0	0	85	1.00	0	0	92	1.00	0	0
	100	0.97	0.01	0	0.03	0	0	100	0.83	0.17	97	1.00	0	0	100	0.99	0.01	0	100	1.00	0	0
Area 7																						
FF.	31	1.00	0	0	0	0	0	31	0.87	0.13	31	1.00	0	0	31	0.95	0.05	0	31	1.00	0	0
GG.	53	0.96	0	0.02	0.02	0	0	53	0.76	0.24	52	1.00	0	0	53	1.00	0	0	53	1.00	0	0
Area 8 - Bella Coola River																						
HH.	100	0.97	0.01	0	0.01	0	0	99	0.84	0.16	97	0.99	0.01	0	100	1.00	0	0	99	1.00	0	0
Area 10																						
II.	100	1.00	0	0	0	0	0	97	0.80	0.20	99	1.00	0	0	100	1.00	0	0	100	1.00	0	0
JJ.	97	0.99	0	0.01	0	0	0	95	0.87	0.13	96	1.00	0	0	96	1.00	0	0	97	1.00	0	0

Location	G3PDH-2 N	*100	*90	MPI[4] N	*a	*b	*c	*d	*e	PGM-1[5] N	*-100	*null	TPI-4 N	*100	*fast
District 101 - Behm Canal - Portland Canal - Boca de Quadra															
A.	99	0.78	0.22	59	0.92	0.06	0	0.02	0	58	0.83	0.17	38	1.00	0
	49	0.83	0.17	10	0.90	0.10	0	0	0	50	0.88	0.12	10	1.00	0
	95	0.83	0.17	98	0.92	0.07	0	0.01	0	98	0.86	0.14	83	0.99	0.01
	52	0.80	0.20	52	0.92	0.08	0	0	0	51	0.78	0.22	52	1.00	0
B.	97	0.79	0.21	58	0.93	0.05	0	0.02	0	97	0.80	0.20	40	1.00	0
C.	105	0.82	0.18	65	0.90	0.09	0	0.01	0	103	0.83	0.17	40	0.99	0.01
D.	100	0.83	0.17	61	0.90	0.09	0	0.01	0	99	0.80	0.20	61	1.00	0
E.	99	0.82	0.18	60	0.91	0.08	0.01	0	0	100	0.87	0.13	60	1.00	0
F.	99	0.80	0.20	63	0.91	0.09	0	0	0	103	0.92	0.08	38	1.00	0
G.	100	0.83	0.17	61	0.86	0.14	0	0	0	101	0.86	0.14	61	1.00	0
	105	0.75	0.25	105	0.85	0.15	0.005	0	0	104	0.86	0.14	40	1.00	0
H.	98	0.81	0.19	60	0.92	0.08	0	0	0	59	0.78	0.22	60	1.00	0
I.	109	0.78	0.22	72	0.89	0.11	0	0	0	111	0.88	0.12	72	1.00	0
	63	0.86	0.14	63	0.92	0.08	0	0	0	63	0.79	0.21	63	1.00	0
J.	97	0.89	0.11	59	0.92	0.08	0	0	0	59	0.86	0.14	40	1.00	0
	52	0.83	0.17	52	0.94	0.06	0	0	0	52	0.83	0.17	29	1.00	0
K.	98	0.84	0.16	62	0.90	0.10	0	0	0	101	0.82	0.18	40	1.00	0
L.	88	0.86	0.14	50	0.86	0.14	0	0	0	90	0.89	0.11	30	1.00	0
M.	124	0.84	0.18	87	0.88	0.12	0	0	0	124	0.83	0.17	60	1.00	0
N.	98	0.84	0.18	57	0.94	0.06	0	0	0	96	0.85	0.15	59	1.00	0
District 102 - Eastern Prince of Wales Island															
O.	104	0.80	0.20	64	0.91	0.09	0	0	0	104	0.92	0.08	41	1.00	0
P.	99	0.83	0.17	60	0.89	0.11	0	0	0	100	0.90	0.10	30	1.00	0
Q.	97	0.77	0.23	58	0.89	0.11	0	0	0	57	0.93	0.07	59	1.00	0
	100	0.70	0.30	100	0.91	0.09	0	0	0	99	0.93	0.07	100	1.00	0
R.	101	0.77	0.23	62	0.91	0.08	0	0	0.01	101	0.90	0.10	61	1.00	0
S.	97	0.81	0.19	59	0.86	0.14	0	0	0	59	0.92	0.08	38	1.00	0
	52	0.81	0.19	52	0.89	0.11	0	0	0	52	0.94	0.06	52	1.00	0
T.	96	0.76	0.24	58	0.89	0.11	0	0	0	58	0.95	0.05	46	1.00	0
U.	100	0.77	0.23	60	0.95	0.05	0	0	0	100	0.94	0.06	40	1.00	0
District 103 - Western Prince of Wales Island															
V.	96	0.85	0.15	58	0.87	0.12	0.01	0	0	99	0.95	0.05	59	1.00	0
W.	92	0.79	0.21	60	0.95	0.05	0	0	0	99	0.86	0.14	35	1.00	0
	100	0.74	0.26	60	0.93	0.07	0	0	0	100	0.94	0.06	60	1.00	0
	53	0.75	0.25	54	0.96	0.05	0	0	0	54	0.93	0.07	50	1.00	0
X.	99	0.81	0.19	60	0.86	0.14	0	0	0	98	1.00	0	40	1.00	0
	47	0.78	0.22	47	0.93	0.06	0	0	0.01	47	1.00	0	48	1.00	0
Y.	83	0.80	0.20	44	0.85	0.15	0	0	0	44	0.93	0.07	44	1.00	0
	54	0.76	0.24	16	0.91	0.09	0	0	0	56	0.91	0.09	16	1.00	0
	53	0.68	0.32	53	0.88	0.11	0	0	0.01	53	0.98	0.02	39	1.00	0
Z.	97	0.80	0.20	60	0.87	0.13	0	0	0	99	0.87	0.13	40	1.00	0
District 105 - Western Sumner Strait															
a.	98	0.74	0.26	58	0.78	0.22	0	0	0	97	0.91	0.09	51	1.00	0
District 107 - Ernest Sound - Bradfield Canal															
b.	91	0.86	0.14	53	0.83	0.17	0	0	0	53	0.81	0.19	40	1.00	0
District 108 - Stikine River															
c.	79	0.84	0.16	39	0.85	0.15	0	0	0	79	0.84	0.16	41	1.00	0
District 109 - Southern Chatham Strait - Western Frederick Sound															
d.	100	0.80	0.20	60	0.93	0.07	0	0	0	100	0.87	0.13	60	1.00	0
	31	0.81	0.19	31	0.90	0.10	0	0	0	31	0.87	0.13	31	1.00	0
e.	61	0.79	0.21	61	0.81	0.18	0.01	0	0	60	0.95	0.05	59	1.00	0
f.	53	0.78	0.22	61	0.84	0.15	0.01	0	0	61	0.84	0.16	61	1.00	0
District 110 - Eastern Frederick Sound															
g.	98	0.84	0.16	60	0.86	0.14	0	0	0	100	0.87	0.13	59	1.00	0
	59	0.79	0.21	61	0.87	0.13	0	0	0	58	0.86	0.14	59	1.00	0
h.	63	0.86	0.14	64	0.87	0.13	0	0	0	65	0.86	0.14	63	1.00	0
i.	27	0.87	0.13	27	0.89	0.11	0	0	0	27	0.93	0.07	27	1.00	0
	40	0.80	0.20	40	0.85	0.15	0	0	0	39	0.95	0.05	40	1.00	0
District 115 - Lynn Canal															
k.	50	0.88	0.12	50	0.87	0.13	0	0	0	50	0.82	0.18	50	1.00	0
l.	96	0.84	0.16	59	0.89	0.11	0	0	0	98	0.78	0.22	57	1.00	0
	58	0.81	0.19	58	0.84	0.16	0	0	0	58	0.71	0.29	59	1.00	0
Area 1 - Northern Queen Charlotte Islands															
m.	75	0.94	0.06	75	0.97	0.03	0	0	0	75	0.85	0.15	75	1.00	0
Area 2 - Western Queen Charlotte Islands															
n.	99	0.77	0.23	100	0.94	0.04	0.01	0	0.01	99	0.86	0.14	100	1.00	0
o.	74	0.87	0.13	75	0.93	0.06	0.01	0	0	75	0.91	0.09	50	1.00	0
p.	100	0.89	0.11	99	0.90	0.04	0.07	0	0	100	0.96	0.05	99	0.99	0.01
Area 2 - Eastern Queen Charlotte Islands															
q.	91	0.88	0.12	91	0.87	0.12	0.01	0	0	91	0.97	0.03	91	1.00	0
r.	81	0.89	0.11	81	0.91	0.09	0	0	0	82	0.91	0.09	82	1.00	0
s.	98	0.90	0.10	100	0.93	0.05	0	0	0.01	100	0.91	0.09	100	1.00	0
t.	82	0.87	0.13	83	0.92	0.04	0	0	0.04	83	0.93	0.07	50	1.00	0
u.	54	0.83	0.17	56	0.85	0.13	0	0	0.02	55	0.93	0.07	57	1.00	0
v.	73	0.84	0.16	74	0.95	0.03	0.01	0	0.01	73	0.88	0.12	74	1.00	0
w.	86	0.86	0.14	89	0.92	0.05	0	0	0.03	89	0.93	0.07	89	1.00	0
x.	84	0.83	0.17	84	0.92	0.05	0	0	0.02	84	0.89	0.11	85	1.00	0
Area 3Z - Portland - Observatory Inlets															
y.	85	0.82	0.18	88	0.91	0.09	0	0	0	67	0.77	0.23	40	1.00	0
z.	90	0.79	0.21	94	0.87	0.10	0	0.04	0	93	0.82	0.18	94	0.98	0.02
AA.	74	0.86	0.14	75	0.91	0.09	0	0	0	73	0.86	0.14	39	1.00	0
	53	0.87	0.13	53	0.88	0.11	0	0.01	0	53	0.81	0.19	53	0.99	0.01
BB.	91	0.79	0.21	94	0.88	0.12	0	0	0	94	0.77	0.23	94	1.00	0
CC.	98	0.90	0.10	98	0.92	0.08	0	0	0	98	0.84	0.16	58	1.00	0
Area 4 - Skeena River															
DD.	98	0.94	0.06	99	0.94	0.06	0	0	0	99	0.63	0.37	99	1.00	0
Area 6															
EE.	87	0.87	0.13	92	0.93	0.07	0	0	0	92	0.85	0.15	34	1.00	0
	99	0.86	0.14	100	0.91	0.08	0	0.01	0	100	0.71	0.29	99	1.00	0
Area 7															
FF.	31	0.81	0.19	31	0.89	0.11	0	0	0	31	0.84	0.16	31	0.98	0.02
GG.	53	0.82	0.18	53	0.85	0.15	0	0	0	53	0.85	0.15	53	1.00	0
Area 8 - Bella Coola River															
HH.	100	0.89	0.11	100	0.95	0.05	0	0	0	98	0.63	0.37	78	1.00	0
Area 10															
II.	97	0.87	0.13	100	0.93	0.07	0	0	0	100	0.85	0.15	98	0.99	0.01
JJ.	96	0.91	0.09	97	0.97	0.03	0	0	0	95	0.88	0.12	94	1.00	0

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Appendix 1. (*Continued*)

Location	PGM-2 N	*-100	*-140	*-40	sIDHP-2 N	*100	*35	*25	*86	*110	sMDH-A1 N	*100	*200	sMDH-A2 N	*100	*65	sAAT-3 N	*100	*90	*110	LDH-C N	*100	*80	CK-B N	*100	*95	FDHG[6] N	*100	*70	TPI-1 N	*-100	*-50	TPI-2 N	*-100	*-260	IDDH-2 N	*100	*140
District 101 - Behm Canal - Portland Canal - Boca de Quadra																																						
A.	100	1.00	0	0	97	0.43	0.29	0.20	0.08	0	60	0.98	0.02	60	0.98	0.02	99	0.52	0.48	0	100	1.00	0	59	1.00	0	60	1.00	0	60	1.00	0	60	1.00	0	39	1.00	0
	50	1.00	0	0	50	0.42	0.43	0.13	0.02	0	10	1.00	0	10	0.95	0.05	47	0.53	0.47	0	49	1.00	0	10	1.00	0	10	1.00	0	10	1.00	0	10	1.00	0	10	1.00	0
	100	1.00	0	0	98	0.37	0.37	0.19	0.07	0	100	0.96	0.04	100	0.99	0.01	98	0.40	0.60	0.01	100	1.00	0	100	1.00	0	100	1.00	0	80	1.00	0	80	1.00	0	70	1.00	0
	52	1.00	0	0	35	0.48	0.34	0.16	0.01	0	52	0.99	0.01	52	0.99	0.01	48	0.54	0.44	0.02	51	1.00	0	50	1.00	0	52	1.00	0	52	1.00	0	52	1.00	0	32	1.00	0
B.	98	1.00	0	0	94	0.39	0.30	0.27	0.04	0	56	1.00	0	58	0.98	0.02	97	0.45	0.53	0.02	98	1.00	0	58	0.99	0.01	40	1.00	0	58	1.00	0	58	1.00	0	38	1.00	0
C.	105	1.00	0	0	93	0.49	0.35	0.12	0.04	0	65	0.94	0.06	64	0.96	0.04	103	0.46	0.54	0	105	0.995	0.005	65	1.00	0	65	1.00	0	65	1.00	0	65	1.00	0	39	1.00	0
D.	101	0.99	0.01	0	99	0.44	0.36	0.15	0.05	0	61	0.96	0.04	61	1.00	0	100	0.47	0.53	0	100	1.00	0	60	0.99	0.01	60	1.00	0	61	1.00	0	61	1.00	0	38	1.00	0
E.	101	1.00	0	0	99	0.42	0.34	0.20	0.04	0	61	0.98	0.02	61	0.99	0.01	101	0.53	0.47	0	101	0.99	0.01	61	1.00	0	61	1.00	0	61	1.00	0	61	1.00	0	61	1.00	0
F.	103	0.995	0.005	0	102	0.47	0.32	0.17	0.04	0	63	0.99	0.01	63	0.98	0.02	103	0.52	0.48	0	102	1.00	0	62	1.00	0	63	1.00	0	62	1.00	0	62	1.00	0	40	1.00	0
G.	101	1.00	0	0	100	0.43	0.32	0.19	0.07	0	61	0.95	0.05	61	0.95	0.05	100	0.63	0.37	0	101	1.00	0	58	1.00	0	59	1.00	0	61	1.00	0	61	1.00	0	37	1.00	0
	105	0.995	0.005	0	101	0.47	0.29	0.14	0.10	0	105	0.98	0.02	105	0.98	0.02	105	0.58	0.42	0	105	1.00	0	105	0.995	0.005	105	1.00	0	105	1.00	0	105	1.00	0	37	0.99	0.01
H.	100	0.99	0.01	0	97	0.47	0.31	0.16	0.06	0	60	0.98	0.02	59	0.97	0.03	96	0.51	0.49	0	99	1.00	0	56	1.00	0	60	1.00	0	60	1.00	0	60	1.00	0	40	1.00	0
I.	111	1.00	0	0	108	0.38	0.28	0.24	0.10	0	72	0.99	0.01	72	0.99	0.01	107	0.57	0.43	0	109	0.99	0.01	71	1.00	0	72	1.00	0	72	1.00	0	72	1.00	0	40	1.00	0
	83	0.98	0.02	0	80	0.43	0.33	0.19	0.05	0	63	0.94	0.06	63	0.98	0.02	63	0.49	0.51	0	63	1.00	0	63	1.00	0	62	1.00	0	63	1.00	0	63	1.00	0	40	1.00	0
J.	100	1.00	0	0	96	0.40	0.31	0.18	0.11	0	60	0.99	0.01	60	0.97	0.03	100	0.55	0.45	0	100	1.00	0	59	1.00	0	58	1.00	0	60	1.00	0	60	1.00	0	37	1.00	0
	52	1.00	0	0	52	0.45	0.27	0.18	0.10	0	52	0.97	0.03	52	0.94	0.06	51	0.53	0.47	0	51	0.99	0.01	51	1.00	0	52	1.00	0	51	1.00	0	51	1.00	0	32	1.00	0
K.	101	1.00	0	0	101	0.39	0.36	0.22	0.03	0	62	0.95	0.05	62	0.98	0.02	99	0.52	0.48	0	102	1.00	0	62	1.00	0	62	1.00	0	62	1.00	0	62	1.00	0	35	1.00	0
L.	90	1.00	0	0	89	0.44	0.30	0.21	0.04	0	50	0.96	0.04	50	0.95	0.05	89	0.48	0.52	0	89	1.00	0	50	1.00	0	50	1.00	0	50	1.00	0	50	1.00	0	40	1.00	0
M.	127	0.996	0.004	0	123	0.44	0.36	0.14	0.07	0	87	0.98	0.02	87	0.95	0.05	125	0.52	0.48	0	125	0.996	0.004	84	1.00	0	86	1.00	0	86	1.00	0	86	1.00	0	40	1.00	0
N.	99	0.98	0.02	0	89	0.41	0.28	0.26	0.05	0	59	0.98	0.02	59	1.00	0	97	0.51	0.48	0.01	100	1.00	0	55	1.00	0	59	1.00	0	59	1.00	0	59	1.00	0	38	1.00	0
District 102 - Eastern Prince of Wales Island																																						
O.	104	1.00	0	0	104	0.48	0.22	0.23	0.07	0	64	0.97	0.03	64	0.96	0.04	103	0.66	0.34	0	103	1.00	0	63	1.00	0	64	1.00	0	63	1.00	0	63	1.00	0	64	0.99	0.01
P.	100	1.00	0	0	100	0.36	0.35	0.19	0.10	0	60	0.93	0.07	60	0.92	0.08	98	0.66	0.34	0	99	1.00	0	60	1.00	0	60	1.00	0	60	1.00	0	60	1.00	0	40	1.00	0
Q.	100	1.00	0	0	100	0.45	0.24	0.19	0.12	0	60	0.93	0.07	60	0.92	0.08	97	0.63	0.37	0	98	1.00	0	58	1.00	0	60	0.99	0.01	59	1.00	0	59	1.00	0	39	1.00	0
	99	1.00	0	0	85	0.39	0.23	0.26	0.12	0	100	0.91	0.09	100	0.91	0.09	98	0.67	0.33	0	99	1.00	0	99	1.00	0	100	1.00	0	97	1.00	0	97	1.00	0	39	1.00	0
R.	102	1.00	0	0	100	0.33	0.33	0.22	0.11	0	62	0.90	0.10	62	0.97	0.03	99	0.58	0.42	0	101	1.00	0	60	1.00	0	40	1.00	0	61	1.00	0	61	1.00	0	40	1.00	0
S.	100	0.99	0.01	0	97	0.42	0.27	0.19	0.12	0	59	0.93	0.07	59	0.95	0.05	99	0.68	0.32	0	97	1.00	0	56	1.00	0	59	1.00	0	58	1.00	0	58	1.00	0	37	1.00	0
	52	1.00	0	0	50	0.42	0.29	0.23	0.08	0	52	0.93	0.07	52	0.99	0.01	52	0.63	0.37	0	52	1.00	0	52	1.00	0	52	1.00	0	52	1.00	0	52	1.00	0	38	1.00	0
T.	103	0.995	0	0.005	98	0.39	0.30	0.24	0.08	0	59	0.97	0.03	59	0.96	0.04	102	0.63	0.37	0	102	1.00	0	60	1.00	0	59	1.00	0	61	1.00	0	61	1.00	0	38	1.00	0
U.	100	1.00	0	0	100	0.57	0.15	0.17	0.11	0	60	0.96	0.04	60	0.96	0.04	98	0.71	0.29	0	98	1.00	0	57	1.00	0	60	1.00	0	60	1.00	0	60	1.00	0	35	1.00	0
District 103 - Western Prince of Wales Island																																						
V.	100	1.00	0	0	98	0.37	0.31	0.25	0.08	0	59	0.93	0.07	59	0.94	0.06	89	0.72	0.28	0	100	1.00	0	57	1.00	0	59	1.00	0	59	1.00	0	59	1.00	0	37	1.00	0
W.	100	0.99	0	0.01	99	0.37	0.29	0.23	0.10	0.01	60	0.97	0.03	60	0.96	0.04	97	0.75	0.25	0	100	1.00	0	60	0.99	0.01	57	1.00	0	60	1.00	0	60	1.00	0	40	1.00	0
	99	1.00	0	0	99	0.40	0.31	0.24	0.05	0	60	0.95	0.05	60	0.94	0.06	97	0.65	0.35	0	100	1.00	0	59	1.00	0	60	1.00	0	60	1.00	0	60	1.00	0	59	1.00	0
	54	1.00	0	0	53	0.40	0.27	0.26	0.07	0	54	0.96	0.04	54	0.99	0.01	53	0.71	0.29	0	54	1.00	0	54	1.00	0	54	1.00	0	54	1.00	0	54	0.99	0.01	40	1.00	0
X.	100	1.00	0	0	98	0.36	0.33	0.20	0.11	0	60	0.88	0.12	60	0.99	0.01	97	0.68	0.32	0	100	1.00	0	60	1.00	0	56	1.00	0	60	1.00	0	60	1.00	0	39	1.00	0
	48	1.00	0	0	42	0.46	0.27	0.19	0.07	0	48	0.94	0.06	47	0.99	0.01	47	0.68	0.32	0	48	1.00	0	48	1.00	0	46	1.00	0	48	1.00	0	48	1.00	0	39	1.00	0
Y.	84	1.00	0	0	31	0.23	0.26	0.44	0.08	0	43	0.95	0.05	44	0.99	0.01	80	0.61	0.39	0	84	1.00	0	42	1.00	0	44	1.00	0	44	1.00	0	44	1.00	0	40	1.00	0
	56	1.00	0	0	56	0.41	0.30	0.21	0.07	0	16	0.87	0.13	16	1.00	0	56	0.56	0.44	0	56	1.00	0	16	1.00	0	16	1.00	0	16	1.00	0	16	1.00	0	---	---	---
	53	0.99	0	0.01	51	0.37	0.29	0.24	0.10	0	53	0.92	0.08	53	0.97	0.03	52	0.74	0.26	0	52	1.00	0	52	1.00	0	52	1.00	0	53	1.00	0	53	1.00	0	37	0.99	0.01
Z.	101	0.99	0	0.01	99	0.46	0.36	0.12	0.06	0	60	0.97	0.03	60	0.97	0.03	100	0.66	0.32	0	99	1.00	0	57	0.99	0.01	58	1.00	0	60	1.00	0	60	1.00	0	59	1.00	0
District 105 - Western Sumner Strait																																						
a.	98	1.00	0	0	98	0.33	0.48	0.15	0.04	0	58	0.97	0.03	58	1.00	0	69	0.57	0.43	0	84	1.00	0	50	1.00	0	56	1.00	0	54	1.00	0	54	1.00	0	40	1.00	0
District 107 - Ernest Sound - Bradfield Canal																																						
b.	93	1.00	0	0	91	0.44	0.37	0.14	0.05	0	55	0.98	0.02	55	0.95	0.05	92	0.51	0.49	0	95	0.99	0.01	55	1.00	0	55	1.00	0	55	1.00	0	55	1.00	0	53	1.00	0
District 108 - Stikine River																																						
c.	61	0.99	0	0.01	80	0.47	0.33	0.13	0.07	0	41	0.96	0.04	40	1.00	0	79	0.54	0.46	0	61	1.00	0	41	1.00	0	41	1.00	0	41	0.98	0.02	41	1.00	0	40	1.00	0
District 109 - Southern Chatham Strait - Western Frederick Sound																																						
d.	100	1.00	0	0	98	0.46	0.37	0.15	0.02	0	60	0.93	0.07	60	0.98	0.02	97	0.73	0.27	0	97	1.00	0	57	1.00	0	60	1.00	0	59	1.00	0	59	1.00	0	34	1.00	0
	31	1.00	0	0	27	0.50	0.26	0.24	0	0	31	0.98	0.02	31	0.98	0.02	30	0.77	0.23	0	30	1.00	0	30	1.00	0	31	1.00	0	31	1.00	0	31	1.00	0	31	1.00	0
e.	61	1.00	0	0	49	0.46	0.35	0.14	0.05	0	61	0.98	0.02	61	1.00	0	60	0.57	0.43	0	60	1.00	0	58	1.00	0	60	1.00	0	61	1.00	0	61	1.00	0	61	1.00	0
f.	61	1.00	0	0	52	0.38	0.35	0.22	0.05	0	61	0.92	0.08	61	1.00	0	60	0.60	0.40	0	61	1.00	0	60	1.00	0	61	1.00	0	61	1.00	0	61	1.00	0	61	0.99	0.01
District 110 - Eastern Frederick Sound																																						
g.	100	1.00	0	0	96	0.37	0.42	0.16	0.05	0	60	0.97	0.03	60	1.00	0	98	0.65	0.35	0	100	1.00	0	59	1.00	0	60	1.00	0	60	1.00	0	60	0.99	0.01	35	1.00	0
	61	1.00	0	0	48	0.41	0.42	0.14	0.04	0	60	0.95	0.05	61	1.00	0	58	0.72	0.28	0	59	1.00	0	60	1.00	0	61	1.00	0	61	1.00	0	61	1.00	0	51	1.00	0
h.	65	0.99	0.01	0	41	0.54	0.28	0.11	0.07	0	65	0.95	0.05	65	1.00	0	65	0.58	0.42	0	65	1.00	0	65	1.00	0	65	0.99	0.01	65	0.99	0.01	65	1.00	0	59	1.00	0
i.	27	1.00	0	0	27	0.39	0.44	0.13	0.04	0	27	0.94	0.06	27	1.00	0	27	0.72	0.28	0	27	1.00	0	26	1.00	0	27	1.00	0	27	1.00	0	27	1.00	0	27	1.00	0
	40	1.00	0	0	36	0.40	0.47	0.10	0.03	0	40	0.96	0.04	40	1.00	0	39	0.64	0.36	0	40	1.00	0	40	1.00	0	40	1.00	0	40	0.97	0.03	40	1.00	0	40	1.00	0
District 115 - Lynn Canal																																						
k.	49	0.97	0	0.03	45	0.38	0.39	0.16	0.08	0	50	0.97	0.03	50	1.00	0	50	0.67	0.33	0	50	1.00	0	50	1.00	0	50	1.00	0	50	1.00	0	50	1.00	0	40	1.00	0
l.	89	1.00	0	0	94	0.55	0.32	0.11	0.01	0.01	60	0.96	0.04	59	1.00	0	98	0.49	0.51	0	100	1.00	0	60	1.00	0	60	1.00	0	60	1.00	0	60	1.00	0	33	1.00	0
	59	1.00	0	0	52	0.56	0.32	0.09	0.04	0	59	1.00	0	59	1.00	0	56	0.36	0.64	0	56	0.98	0.02	57	1.00	0	58	1.00	0	59	1.00	0	59	1.00	0	58	0.99	0.01
Area 1 - Northern Queen Charlotte Islands																																						
m.	75	1.00	0	0	66	0.33	0.25	0.23	0.18	0	74	0.93	0.07	75	0.99	0.01	74	0.53	0.47	0	75	1.00	0	75	1.00	0	74	1.00	0	75	1.00	0	75	1.00	0	43	1.00	0
Area 2 - Western Queen Charlotte Islands																																						
n.	99	1.00	0	0	79	0.23	0.11	0.47	0.18	0	100	0.81	0.19	100	0.99	0.01	100	0.68	0.32	0	100	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0	98	1.00	0
o.	75	1.00	0	0	61	0.26	0.35	0.29	0.10	0	75	0.91	0.09	75	0.97	0.03	75	0.57	0.43	0	75	1.00	0	75	1.00	0	75	1.00	0	75	1.00	0	75	1.00	0	74	1.00	0
p.	100	1.00	0	0	97	0.28	0.32	0.36	0.07	0	100	0.83	0.17	100	0.98	0.02	97	0.65	0.35	0	99	1.00	0	99	0.98	0.02	100	1.00	0	99	1.00	0	99	1.00	0	99	1.00	0
Area 2 - Eastern Queen Charlotte Islands																																						
q.	91	1.00	0	0	69	0.25	0.36	0.34	0.04	0	91	0.93	0.07	91	0.99	0.01	89	0.70	0.30	0	91	1.00	0	91	1.00	0	91	1.00	0	91	1.00	0	91	0.99	0.01	91	0.99	0.01
r.	82	1.00	0	0	57	0.30	0.28	0.34	0.08	0	82	0.91	0.09	82	1.00	0	82	0.66	0.34	0	82	1.00	0	82	1.00	0	40	1.00	0	82	1.00	0	82	1.00	0	34	1.00	0
s.	100	1.00	0	0	79	0.30	0.39	0.21	0.09	0	100	0.91	0.09	99	0.98	0.02	99	0.56	0.44	0	99	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0
t.	83	1.00	0	0	72	0.25	0.32	0.28	0.15	0	82	0.92	0.08	83	0.99	0.01	83	0.63	0.37	0	83	1.00	0	82	1.00	0	83	1.00	0	50	1.00	0	50	0.99	0.01	75	1.00	0
u.	57	1.00	0	0	46	0.35	0.27	0.20	0.18	0	57	0.92	0.08	56	0.99	0.01	57	0.70	0.30	0	57	1.00	0	57	1.00	0	57	1.00	0	57	1.00	0	57	1.00	0	54	1.00	0
v.	74	1.00	0	0	68	0.31	0.35	0.17	0.18	0	73	0.94	0.06	72	0.98	0.02	69	0.73	0.27	0	74	1.00	0	74	1.00	0	74	1.00	0	74	1.00	0	74	1.00	0	74	1.00	0
w.	89	1.00	0	0	83	0.27	0.33	0.31	0.10	0	89	0.89	0.11	89	0.98	0.02	83	0.70	0.30	0	88	1.00	0	88	1.00	0	78	1.00	0	89	1.00	0	89	1.00	0	88	0.99	0.01
x.	85	1.00	0	0	83	0.30	0.28	0.25	0.17	0	85	0.86	0.14	85	0.99	0.01	85	0.74	0.26	0	85	1.00	0	85	0.99	0.01	85	1.00	0	85	1.00	0	85	1.00	0	85	1.00	0
Area 3Z - Portland - Observatory Inlets																																						
y.	88	1.00	0	0	76	0.45	0.32	0.19	0.03	0	86	0.98	0.02	88	0.98	0.02	83	0.52	0.48	0	88	1.00	0	86	1.00	0	88	1.00	0	88	1.00	0	88	1.00	0	40	1.00	0
z.	95	1.00	0	0	70	0.49	0.29	0.16	0.06	0	94	0.96	0.04	95	0.99	0.01	89	0.45	0.55	0	94	1.00	0	91	1.00	0	94	1.00	0	94	1.00	0	94	1.00	0	88	1.00	0
AA.	75	1.00	0	0	60	0.36	0.37	0.20	0.08	0	75	0.97	0.03	75	1.00	0	75	0.47	0.53	0	75	1.00	0	74	1.00	0	75	1.00	0	75	1.00	0	75	1.00	0	74	1.00	0
	53	1.00	0	0	49	0.36	0.33	0.26	0.06	0	52	0.94	0.06	53	0.99	0.01	50	0.45	0.55	0	53	1.00	0	53	1.00	0	53	1.00	0	53	1.00	0	53	1.00	0	52	1.00	0
BB.	94	1.00	0	0	87	0.52	0.31	0.14	0.02	0	94	0.99	0.01	94	0.98	0.02	83	0.49	0.51	0	94	1.00	0	94	1.00	0	94	1.00	0	94	1.00	0	94	1.00	0	39	1.00	0
CC.	98	0.99	0.01	0	85	0.44	0.26	0.28	0.02	0	98	0.99	0.01	98	0.94	0.06	94	0.54	0.46	0	97	1.00	0	98	1.00	0	98	1.00	0	98	1.00	0	98	1.00	0	40	1.00	0
Area 4 - Skeena River																																						
DD.	99	1.00	0	0	78	0.20	0.32	0.41	0.07	0	99	0.90	0.10	99	1.00	0	94	0.33	0.67	0	99	0.99	0.01	99	1.00	0	99	1.00	0	99	1.00	0	99	1.00	0	39	1.00	0
Area 6																																						
EE.	92	0.99	0	0.01	52	0.46	0.37	0.13	0.05	0	90	0.97	0.03	91	0.98	0.02	81	0.46	0.54	0	91	1.00	0	88	1.00	0	84	1.00	0	82	1.00	0	82	1.00	0	52	1.00	0
	100	0.99	0	0.01	77	0.36	0.44	0.13	0.07	0	100	0.99	0.01	100	0.99	0.01	93	0.49	0.51	0	100	0.99	0.01	97	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0	80	1.00	0
Area 7																																						
FF.	31	1.00	0	0	---	---	---	---	---	---	31	0.95	0.05	31	0.97	0.03	31	0.45	0.55	0	30	1.00	0	30	1.00	0	31	1.00	0	31	1.00	0	31	1.00	0	31	1.00	0
GG.	53	0.98	0	0.02	45	0.36	0.37	0.17	0.11	0	53	0.99	0.01	53	1.00	0	52	0.44	0.56	0	53	1.00	0	53	1.00	0	53	1.00	0	53	1.00	0	53	1.00	0	53	1.00	0
Area 8 - Bella Coola River																																						
HH.	100	0.98	0.02	0	69	0.39	0.43	0.12	0.06	0	100	0.95	0.05	100	0.99	0.01	100	0.50	0.50	0	99	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0	100	1.00	0
Area 10																																						
II.	100	1.00	0	0	---	---	---	---	---	---	100	0.98	0.02	99	1.00	0	89	0.54	0.46	0	100	0.96	0.04	100	1.00	0	98	1.00	0	100	1.00	0	100	1.00	0	93	0.99	0.01
JJ.	97	1.00	0	0	71	0.29	0.52	0.16	0.03	0	98	0.97	0.03	95	0.99	0.01	81	0.59	0.41	0	96	0.98	0.02	96	1.00	0	93	1.00	0	97	1.00	0	97	1.00	0	96	1.00	0

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Appendix 1. (*Concluded*)

Location	PEPA (GL) N	PEPA *100	PEPA *92	sMEP-1 N	sMEP-1 *100	sMEP-1 *90	CK-A1 N	CK-A1 *100	CK-A1 *120	CK-A1 *70	CK-A2[7] N	CK-A2 *100	CK-A2 *105	CK-A2 *93	GPI-B1,2 N	GPI-B1,2 *100	GPI-B1,2 *145	G3PDH-3 N	G3PDH-3 *100	G3PDH-3 *110
District 101 - Bohm Canal - Portland Canal - Boca de Quadra																				
A.	99	1.00	0	100	1.00	0	99	1.00	0	0	99	1.00	0	0	100	1.00	0	59	1.00	0
	50	0.99	0.01	50	1.00	0	50	1.00	0	0	50	1.00	0	0	50	1.00	0	10	1.00	0
	34	1.00	0	97	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	97	1.00	0
	52	1.00	0	51	1.00	0	52	1.00	0	0	52	1.00	0	0	52	1.00	0	52	1.00	0
B.	97	1.00	0	98	1.00	0	98	1.00	0	0	98	1.00	0	0	98	1.00	0	57	1.00	0
C.	105	1.00	0	105	0.99	0.01	105	1.00	0	0	105	1.00	0	0	104	1.00	0	65	1.00	0
D.	101	1.00	0	100	1.00	0	101	1.00	0	0	100	1.00	0	0	101	1.00	0	61	1.00	0
E.	100	1.00	0	99	0.99	0.01	101	1.00	0	0	101	1.00	0	0	101	1.00	0	60	1.00	0
F.	103	1.00	0	102	1.00	0	102	1.00	0	0	102	0.995	0	0.005	103	1.00	0	61	1.00	0
G.	101	1.00	0	100	1.00	0	98	0.99	0	0.01	98	1.00	0	0	101	1.00	0	60	1.00	0
	104	0.995	0.005	105	1.00	0	104	1.00	0	0	104	1.00	0	0	105	1.00	0	105	1.00	0
H.	58	1.00	0	60	1.00	0	100	1.00	0	0	100	1.00	0	0	98	1.00	0	59	1.00	0
I.	111	1.00	0	111	1.00	0	111	1.00	0	0	111	1.00	0	0	111	0.995	0.005	70	1.00	0
	40	1.00	0	63	1.00	0	63	1.00	0	0	63	1.00	0	0	63	0.99	0.01	63	1.00	0
J.	98	0.99	0.01	60	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	58	1.00	0
	51	1.00	0	51	1.00	0	52	1.00	0	0	52	1.00	0	0	52	1.00	0	52	1.00	0
K.	99	1.00	0	101	0.99	0.01	102	1.00	0	0	102	1.00	0	0	101	1.00	0	59	1.00	0
L.	90	1.00	0	90	1.00	0	90	1.00	0	0	90	1.00	0	0	90	1.00	0	49	1.00	0
M.	125	1.00	0	127	1.00	0	127	1.00	0	0	127	1.00	0	0	126	1.00	0	66	1.00	0
N.	99	1.00	0	100	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	58	1.00	0
District 102 - Eastern Prince of Wales Island																				
O.	104	1.00	0	103	1.00	0	103	1.00	0	0	103	1.00	0	0	104	1.00	0	64	1.00	0
P.	60	1.00	0	98	1.00	0	60	1.00	0	0	60	0.99	0.01	0	100	1.00	0	60	1.00	0
Q.	99	1.00	0	100	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	58	1.00	0
	60	1.00	0	99	1.00	0	96	1.00	0	0	96	0.99	0.01	0	100	1.00	0	100	1.00	0
R.	78	1.00	0	97	1.00	0	97	1.00	0	0	97	1.00	0	0	98	1.00	0	62	1.00	0
S.	59	1.00	0	99	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	59	1.00	0
	52	1.00	0	52	1.00	0	51	1.00	0	0	52	1.00	0	0	51	1.00	0	51	1.00	0
T.	99	1.00	0	62	1.00	0	103	1.00	0	0	103	0.995	0	0.005	103	1.00	0	57	1.00	0
U.	99	1.00	0	100	1.00	0	100	1.00	0	0	99	1.00	0	0	100	1.00	0	60	1.00	0
District 103 - Western Prince of Wales Island																				
V.	41	1.00	0	100	1.00	0	99	1.00	0	0	99	1.00	0	0	100	1.00	0	58	1.00	0
W.	97	1.00	0	100	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	54	1.00	0
	98	1.00	0	100	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	60	1.00	0
	48	1.00	0	54	0.98	0.02	54	1.00	0	0	54	1.00	0	0	54	1.00	0	54	1.00	0
X.	98	1.00	0	60	1.00	0	99	1.00	0	0	99	1.00	0	0	94	1.00	0	60	1.00	0
	42	1.00	0	48	1.00	0	48	1.00	0	0	48	1.00	0	0	48	1.00	0	47	1.00	0
Y.	72	1.00	0	44	1.00	0	72	1.00	0	0	72	1.00	0	0	64	1.00	0	44	1.00	0
	58	1.00	0	55	1.00	0	56	1.00	0	0	56	1.00	0	0	56	1.00	0	16	1.00	0
	36	1.00	0	53	1.00	0	53	1.00	0	0	53	1.00	0	0	53	1.00	0	53	1.00	0
Z.	97	1.00	0	101	1.00	0	96	1.00	0	0	96	1.00	0	0	91	1.00	0	57	1.00	0
District 105 - Western Sumner Strait																				
a.	96	1.00	0	98	1.00	0	98	1.00	0	0	98	1.00	0	0	98	1.00	0	58	1.00	0
District 107 - Ernest Sound - Bradfield Canal																				
b.	94	1.00	0	95	0.99	0.01	95	1.00	0	0	95	1.00	0	0	95	1.00	0	51	1.00	0
District 108 - Stikine River																				
c.	40	1.00	0	81	1.00	0	81	1.00	0	0	81	1.00	0	0	81	1.00	0	39	1.00	0
District 109 - Southern Chatham Strait - Western Frederick Sound																				
d.	98	1.00	0	100	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	50	1.00	0
	31	1.00	0	30	1.00	0	31	1.00	0	0	31	1.00	0	0	30	1.00	0	31	1.00	0
e.	39	1.00	0	61	1.00	0	61	1.00	0	0	61	1.00	0	0	61	1.00	0	81	1.00	0
f.	40	1.00	0	60	1.00	0	61	1.00	0	0	61	1.00	0	0	61	1.00	0	54	1.00	0
District 110 - Eastern Frederick Sound																				
g.	100	1.00	0	100	1.00	0	100	0.99	0	0.01	100	1.00	0	0	100	0.99	0.01	60	1.00	0
	38	1.00	0	61	1.00	0	58	1.00	0	0	61	1.00	0	0	52	1.00	0	60	1.00	0
h.	40	1.00	0	63	1.00	0	65	0.99	0.01	0	65	1.00	0	0	65	1.00	0	64	1.00	0
i.	27	1.00	0	27	1.00	0	20	1.00	0	0	20	1.00	0	0	27	0.96	0.02	27	1.00	0
	36	1.00	0	40	1.00	0	29	1.00	0	0	29	1.00	0	0	33	1.00	0	40	1.00	0
District 115 - Lynn Canal																				
k.	50	1.00	0	50	1.00	0	50	1.00	0	0	50	1.00	0	0	50	1.00	0	50	1.00	0
l.	98	1.00	0	98	1.00	0	100	1.00	0	0	100	0.99	0	0.01	100	1.00	0	59	1.00	0
	58	1.00	0	59	1.00	0	59	1.00	0	0	59	1.00	0	0	59	1.00	0	58	1.00	0
Area 1 - Northern Queen Charlotte Islands																				
m.	39	1.00	0	75	1.00	0	75	1.00	0	0	75	1.00	0	0	74	1.00	0	75	1.00	0
Area 2 - Western Queen Charlotte Islands																				
n.	98	1.00	0	99	1.00	0	99	1.00	0	0	99	1.00	0	0	100	1.00	0	100	1.00	0
o.	40	1.00	0	75	1.00	0	75	1.00	0	0	75	1.00	0	0	75	1.00	0	75	1.00	0
p.	95	1.00	0	98	1.00	0	98	1.00	0	0	98	1.00	0	0	98	1.00	0	100	1.00	0
Area 2 - Eastern Queen Charlotte Islands																				
q.	40	1.00	0	91	1.00	0	91	1.00	0	0	91	1.00	0	0	91	1.00	0	91	1.00	0
r.	38	1.00	0	82	1.00	0	82	1.00	0	0	82	1.00	0	0	82	1.00	0	81	1.00	0
s.	39	1.00	0	100	1.00	0	100	1.00	0	0	100	1.00	0	0	100	1.00	0	100	0.96	0.04
t.	79	1.00	0	83	1.00	0	83	1.00	0	0	83	1.00	0	0	83	1.00	0	83	1.00	0
u.	40	1.00	0	57	1.00	0	57	1.00	0	0	57	1.00	0	0	57	1.00	0	56	1.00	0
v.	35	1.00	0	74	1.00	0	74	1.00	0	0	74	1.00	0	0	74	1.00	0	74	1.00	0
w.	37	1.00	0	88	1.00	0	87	1.00	0	0	89	1.00	0	0	89	0.99	0.01	89	0.99	0.01
x.	34	1.00	0	85	1.00	0	85	1.00	0	0	84	1.00	0	0	85	1.00	0	84	1.00	0
Area 3Z - Portland - Observatory Inlets																				
y.	87	1.00	0	87	1.00	0	84	1.00	0	0	84	1.00	0	0	88	1.00	0	84	1.00	0
z.	54	1.00	0	94	1.00	0	90	1.00	0	0	90	1.00	0	0	95	1.00	0	91	1.00	0
AA.	40	1.00	0	75	1.00	0	75	1.00	0	0	75	1.00	0	0	74	1.00	0	75	1.00	0
	53	0.99	0.01	53	1.00	0	53	1.00	0	0	53	1.00	0	0	52	1.00	0	53	1.00	0
BB.	94	1.00	0	94	1.00	0	92	1.00	0	0	92	1.00	0	0	93	1.00	0	93	1.00	0
CC.	96	1.00	0	98	1.00	0	98	1.00	0	0	98	1.00	0	0	98	1.00	0	98	1.00	0
Area 4 - Skeena River																				
DD.	37	1.00	0	99	1.00	0	99	0.99	0.01	0	99	1.00	0	0	98	1.00	0	98	1.00	0
Area 6																				
EE.	38	1.00	0	91	1.00	0	77	1.00	0	0	77	1.00	0	0	91	1.00	0	90	1.00	0
	96	1.00	0	99	0.99	0.01	94	1.00	0	0	94	1.00	0	0	99	1.00	0	100	1.00	0
Area 7																				
FF.	31	1.00	0	31	1.00	0	30	1.00	0	0	30	1.00	0	0	31	1.00	0	31	1.00	0
GG.	53	1.00	0	53	1.00	0	53	1.00	0	0	53	1.00	0	0	53	1.00	0	53	1.00	0
Area 8 - Bella Coola River																				
HH.	40	1.00	0	99	1.00	0	99	1.00	0	0	99	1.00	0	0	99	1.00	0	100	1.00	0
Area 10																				
II.	39	1.00	0	100	1.00	0	98	0.99	0.01	0	98	1.00	0	0	90	1.00	0	97	1.00	0
JJ.	57	1.00	0	95	1.00	0	98	1.00	0	0	96	1.00	0	0	89	1.00	0	96	1.00	0

Location	mAH-3 N	mAH-3 *100	mAH-3 *124	sAH N	sAH *100	sAH *90	sAH *110	mAH-1,2 N	mAH-1,2 *100	mAH-1,2 *50	CK-C1[8] N	CK-C1 *100	CK-C1 *slow	TPI-3[9] N	TPI-3 *100	TPI-3 *slow	FH N	FH *100	FH *slow	FH *fast
District 101 - Bohm Canal - Portland Canal - Boca de Quadra																				
A.	51	0.29	0.71	58	1.00	0	0	47	0.96	0.04	59	1.00	0	38	1.00	0	60	0.97	0.02	0.01
	48	0.33	0.67	50	1.00	0	0	10	1.00	0	10	1.00	0	10	1.00	0	10	0.90	0.10	0
	89	0.38	0.62	70	1.00	0	0	89	0.96	0.04	97	1.00	0	79	1.00	0	100	0.98	0.02	0
	33	0.48	0.52	39	1.00	0	0	31	0.95	0.05	49	1.00	0	52	1.00	0	52	0.94	0.05	0.01
B.	52	0.30	0.70	57	1.00	0	0	25	0.94	0.06	56	1.00	0	40	1.00	0	58	1.00	0	0
C.	45	0.37	0.63	65	1.00	0	0	35	1.00	0	64	1.00	0	40	1.00	0	65	0.98	0.02	0
D.	60	0.44	0.56	61	0.99	0	0.01	47	0.93	0.07	59	1.00	0	61	0.99	0.01	61	0.98	0.02	0
E.	96	0.40	0.60	99	0.99	0.01	0	59	0.97	0.03	61	1.00	0	60	1.00	0	61	0.98	0.02	0
F.	93	0.42	0.58	97	0.99	0.01	0	52	0.99	0.01	56	1.00	0	38	1.00	0	62	0.99	0.01	0
G.	60	0.43	0.57	40	1.00	0	0	54	0.97	0.03	59	1.00	0	60	1.00	0	61	0.98	0.02	0
	41	0.39	0.61	32	1.00	0	0	42	0.99	0.01	103	1.00	0	39	1.00	0	104	0.995	0.005	0
H.	44	0.31	0.69	38	1.00	0	0	36	0.99	0.01	56	1.00	0	60	0.99	0.01	59	0.97	0.03	0
I.	59	0.53	0.47	69	1.00	0	0	60	0.96	0.04	69	1.00	0	72	1.00	0	72	0.95	0.04	0.01
	29	0.45	0.55	58	1.00	0	0	24	0.96	0.04	63	1.00	0	63	0.99	0.01	62	0.92	0.08	0
J.	47	0.41	0.59	37	1.00	0	0	45	0.92	0.08	67	1.00	0	40	1.00	0	60	0.96	0.04	0
	48	0.54	0.46	32	1.00	0	0	48	0.98	0.02	51	1.00	0	29	1.00	0	51	0.94	0.05	0.01
K.	94	0.40	0.60	99	0.99	0.01	0	15	1.00	0	62	1.00	0	40	1.00	0	60	0.97	0.03	0
L.	39	0.33	0.67	—	—	—	—	49	1.00	0	47	1.00	0	30	1.00	0	50	0.98	0.02	0
M.	66	0.33	0.67	67	0.99	0.01	0.01	66	0.99	0.01	83	1.00	0	60	1.00	0	87	0.95	0.05	0.01
N.	41	0.48	0.52	44	1.00	0	0	38	0.97	0.03	48	1.00	0	59	0.99	0.01	59	0.99	0.01	0
District 102 - Eastern Prince of Wales Island																				
O.	62	0.38	0.62	50	0.99	0.01	0	55	1.00	0	63	1.00	0	41	1.00	0	63	0.97	0.03	0
P.	53	0.56	0.44	40	1.00	0	0	48	1.00	0	60	1.00	0	30	1.00	0	58	0.96	0.04	0
Q.	49	0.48	0.52	40	1.00	0	0	47	1.00	0	58	1.00	0	59	1.00	0	60	0.93	0.07	0
	65	0.48	0.52	19	1.00	0	0	73	1.00	0	87	1.00	0	99	0.99	0.01	100	0.95	0.05	0
R.	43	0.44	0.56	52	0.99	0.01	0	45	1.00	0	59	1.00	0	61	0.99	0.01	61	0.94	0.05	0.01
S.	51	0.40	0.60	36	1.00	0	0	43	0.99	0.01	54	1.00	0	38	1.00	0	55	0.95	0.05	0
	41	0.45	0.55	49	0.99	0	0.01	45	1.00	0	52	1.00	0	52	1.00	0	51	0.95	0.05	0
T.	48	0.45	0.55	35	1.00	0	0	38	1.00	0	60	1.00	0	46	1.00	0	62	0.94	0.06	0
U.	53	0.42	0.58	—	—	—	—	48	0.99	0.01	57	0.99	0.01	40	1.00	0	60	0.96	0.04	0
District 103 - Western Prince of Wales Island																				
V.	86	0.37	0.63	77	1.00	0	0	44	1.00	0	56	1.00	0	59	0.99	0.01	57	0.95	0.05	0
W.	41	0.46	0.54	40	1.00	0	0	33	1.00	0	58	1.00	0	39	1.00	0	60	0.98	0.02	0
	95	0.41	0.59	96	1.00	0	0	48	1.00	0	52	1.00	0	60	1.00	0	60	0.99	0.01	0
	52	0.43	0.57	54	1.00	0	0	30	0.98	0.02	47	1.00	0	50	1.00	0	54	0.99	0.01	0
X.	43	0.48	0.52	36	1.00	0	0	49	1.00	0	41	1.00	0	40	1.00	0	60	0.93	0.07	0
	19	0.37	0.63	39	1.00	0	0	20	1.00	0	45	1.00	0	48	1.00	0	45	0.94	0.06	0
Y.	25	0.44	0.56	43	1.00	0	0	24	1.00	0	40	1.00	0	44	1.00	0	44	0.98	0.02	0
	56	0.46	0.54	40	1.00	0	0	—	—	—	16	1.00	0	16	1.00	0	15	0.94	0.06	0
	44	0.50	0.50	39	1.00	0	0	41	0.99	0.01	50	1.00	0	39	1.00	0	53	0.97	0.03	0
Z.	—	—	—	57	1.00	0	0	—	—	—	50	1.00	0	50	0.99	0.01	57	0.97	0.03	0
District 105 - Western Sumner Strait																				
a.	53	0.34	0.66	40	1.00	0	0	51	1.00	0	46	1.00	0	53	1.00	0	58	1.00	0	0
District 107 - Ernest Sound - Bradfield Canal																				
b.	82	0.41	0.59	92	1.00	0	0	47	0.98	0.02	54	1.00	0	40	1.00	0	54	0.96	0.04	0
District 108 - Stikine River																				
c.	27	0.57	0.43	28	1.00	0	0	30	0.98	0.02	40	1.00	0	41	1.00	0	41	0.95	0.05	0
District 109 - Southern Chatham Strait - Western Frederick Sound																				
d.	96	0.51	0.49	80	1.00	0	0	58	1.00	0	55	0.99	0.01	59	1.00	0	60	0.95	0.05	0
	29	0.38	0.62	30	1.00	0	0	29	1.00	0	30	0.97	0.03	31	1.00	0	31	0.94	0.06	0
e.	—	—	—	60	1.00	0	0	—	—	—	59	1.00	0	60	1.00	0	60	0.98	0.02	0
f.	54	0.40	0.60	55	1.00	0	0	—	—	—	60	1.00	0	61	1.00	0	61	0.99	0.01	0
District 110 - Eastern Frederick Sound																				
g.	96	0.53	0.47	57	1.00	0	0	56	1.00	0	58	1.00	0	60	1.00	0	60	1.00	0	0
	39	0.50	0.50	61	1.00	0	0	31	1.00	0	59	1.00	0	61	1.00	0	60	0.98	0.02	0
h.	42	0.40	0.60	43	1.00	0	0	47	1.00	0	64	1.00	0	62	0.99	0.01	64	0.98	0.02	0
i.	—	—	—	27	1.00	0	0	—	—	—	27	1.00	0	27	1.00	0	27	1.00	0	0
	—	—	—	40	1.00	0	0	—	—	—	40	1.00	0	40	1.00	0	40	0.96	0.04	0
District 115 - Lynn Canal																				
k.	43	0.40	0.60	46	1.00	0	0	40	1.00	0	50	1.00	0	50	1.00	0	50	0.95	0.05	0
l.	42	0.68	0.32	37	1.00	0	0	52	1.00	0	59	1.00	0	57	1.00	0	60	0.99	0.01	0
	47	0.55	0.45	59	1.00	0	0	58	1.00	0	56	1.00	0	59	1.00	0	59	0.99	0.01	0
Area 1 - Northern Queen Charlotte Islands																				
m.	73	0.45	0.55	72	0.98	0	0.02	66	0.99	0.01	72	1.00	0	75	1.00	0	75	1.00	0	0
Area 2 - Western Queen Charlotte Islands																				
n.	89	0.33	0.67	92	1.00	0	0	88	1.00	0	100	1.00	0	100	1.00	0	98	0.93	0.07	0
o.	64	0.34	0.66	56	1.00	0	0	56	0.98	0.02	73	1.00	0	50	1.00	0	73	0.95	0.05	0
p.	61	0.45	0.55	60	1.00	0	0	84	0.98	0.02	96	1.00	0	99	1.00	0	97	0.98	0.02	0
Area 2 - Eastern Queen Charlotte Islands																				
q.	82	0.37	0.63	80	1.00	0	0	83	0.98	0.02	91	1.00	0	91	1.00	0	91	0.94	0.06	0
r.	76	0.30	0.70	77	1.00	0	0	69	0.99	0.01	82	1.00	0	82	1.00	0	82	0.90	0.10	0
s.	—	—	—	95	0.98	0	0.02	—	—	—	97	1.00	0	100	0.99	0.01	99	0.90	0.10	0
t.	76	0.30	0.70	72	1.00	0	0	72	0.97	0.03	76	1.00	0	50	1.00	0	78	0.96	0.04	0
u.	37	0.32	0.68	43	1.00	0	0	43	0.99	0.01	48	1.00	0	57	1.00	0	57	0.96	0.04	0
v.	74	0.26	0.74	68	1.00	0	0	71	0.95	0.05	57	1.00	0	74	1.00	0	73	0.97	0.03	0
w.	73	0.31	0.69	79	1.00	0	0	71	0.98	0.02	85	1.00	0	89	1.00	0	88	0.95	0.05	0
x.	71	0.30	0.70	84	1.00	0	0	64	0.98	0.02	70	1.00	0	85	1.00	0	85	0.98	0.02	0
Area 3Z - Portland - Observatory Inlets																				
y.	57	0.45	0.55	84	1.00	0	0	59	0.99	0.01	77	1.00	0	36	1.00	0	87	0.97	0.03	0.01
z.	79	0.39	0.61	73	1.00	0	0	84	0.93	0.07	—	—	—	94	1.00	0	94	0.98	0.02	0
AA.	68	0.50	0.50	33	1.00	0	0	64	0.94	0.06	72	0.99	0.01	40	1.00	0	75	0.99	0.01	0
	42	0.32	0.68	51	1.00	0	0	45	0.92	0.08	48	1.00	0	53	1.00	0	53	1.00	0	0
BB.	72	0.44	0.56	89	0.99	0	0.01	67	0.99	0.01	85	1.00	0	94	1.00	0	83	0.95	0.05	0
CC.	90	0.44	0.56	93	1.00	0	0	86	0.98	0.02	79	1.00	0	58	1.00	0	98	0.98	0.02	0
Area 4 - Skeena River																				
DD.	—	—	—	96	1.00	0	0	70	0.95	0.05	96	0.97	0.03	99	1.00	0	99	0.97	0.03	0
Area 6																				
EE.	—	—	—	87	1.00	0	0	—	—	—	85	1.00	0	34	1.00	0	91	0.98	0.02	0
	—	—	—	98	1.00	0	0	—	—	—	95	1.00	0	100	1.00	0	99	0.97	0.03	0
Area 7																				
FF.	24	0.25	0.75	25	1.00	0	0	—	—	—	30	1.00	0	31	1.00	0	31	1.00	0	0
GG.	42	0.35	0.65	51	1.00	0	0	44	1.00	0	51	1.00	0	53	1.00	0	53	1.00	0	0
Area 8 - Bella Coola River																				
HH.	—	—	—	83	1.00	0	0	—	—	—	99	1.00	0	79	1.00	0	100	0.98	0.02	0
Area 10																				
II.	80	0.22	0.78	79	1.00	0	0	71	0.95	0.05	83	1.00	0	98	1.00	0	100	0.97	0.03	0
JJ.	45	0.23	0.77	77	1.00	0	0	—	—	—	67	1.00	0	94	1.00	0	95	0.98	0.02	0

[1]One fast heterozygote (**100/*140*) found at Mussel was pooled with the common allele.
[2]We found one and three slow heterozygotes at Nekite Channel and Nekite River, respectively; one fast heterozygote at Traitors 1988; one fast heterozygote at Elena Bay; one slow heterozygote at *LDH-A2** at Kitimat 1988. These variants were pooled with the common allele.
[3]Two buffers are required to resolve alleles; mobilities for alleles "*a*, *b*, *c*, *d*, and *e*" are **−100* and **100*, **−126* and **100*, **−127* and **59*, **−146* and **59*, and **−72* and **110*, for gel buffers CA5.75 and TG (or R), respectively.
[4]Two buffers are required to resolve alleles; mobilities for alleles "*a*, *b*, *c*, *d*, and *e*" are **100* and **100*, **92* and **94*, **92* and **91*, **81* and **86*, and **86* and **94* for gel buffers CA7 and MF, respectively.
[5]Phenotypic frequencies listed: **100* includes both **−100/*−100* and **−100/*null* phenotypes; **null* includes only **null/*null* phenotypes. One **−100/*−180* heterozygote at Disappearance 1988 and one **−180/*−180* or **−180/*null* phenotype at Disappearance 1988 were found. These variants were pooled with the common allele.
[6]Four heterozygotes (**100/*125*) found at Herman Creek 1990 were pooled with the common allele.
[7]One very slow heterozygote found at Tombstone 1986 was pooled with the common allele.
[8]Three slow *CK-C2** heterozygotes found at Donkey 1990 were pooled with the common allele.
[9]Two fast heterozygotes found at Breezy Bay 1987 were pooled with the common allele.

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APPENDIX 2. Log-likelihood ratio analysis: regional comparisons of chum salmon from southeast Alaska and northern British Columbia.

		Within Regions								
Locus		South SE AK. Northern B.C.	Prince of Wales Is.	Central/ Northern SE	NW Queen Charlotte	SE Queen Charlotte Is.	Central BC	Total within	Total among	Total
*sAAT-1,2**	df	38	22	18	10	10	12	110	10	120
	G	24.96	9.32	86.93***	39.69***	4.67	14.73	180.30***	211.45***	391.75***
*mAAT-1**	df	38	22	18	10	10	12	110	10	120
	G	73.11***	78.28***	47.91***	62.59***	13.17	91.75***	366.81***	567.21***	934.02***
*ALAT**	df	38	22	18	10	10	12	110	10	120
	G	69.79**	36.50*	26.95	57.84***	9.71	49.26***	250.05***	98.19***	348.24***
*ESTD-1**	df	38	22	18	10	10	12	110	10	120
	G	19.94	52.98***	18.85	23.98**	11.90	31.49**	159.14**	294.19***	453.33***
*mIDHP-1**	df	19	11	9	5	5	6	55	5	60
	G	32.46	31.38***	9.62	15.10**	5.81	36.93***	131.30***	236.35***	367.65***
*LDH-A1**	df	38	22	18	10	10	12	110	10	120
	G	17.05	31.27	6.04	12.55*	10.48	29.67**	107.06	70.65***	177.71***
*LDH-B2**	df	19	11	9	5	5	6	55	5	60
	G	34.40	14.18	17.76*	46.38***	2.54	6.90	122.16***	215.65***	337.81***
*PEPB-1**	df	76	44	36	20	20	24	220	20	240
	G	72.26	42.75	45.36	44.47**	18.33	67.46***	290.63***	283.71***	574.34***
*sMDH-B1,2**	df	76	44	36	20	20	24	220	20	240
	G	98.37***	62.26*	11.83	42.21**	22.28	51.04**	287.99**	166.79***	454.78***
*mMEP-2**	df	19	11	9	5	5	6	55	5	60
	G	31.92*	20.92*	16.68	45.70***	6.87	26.70***	148.79***	155.25***	304.04***
*GPI-A**	df	38	22	18	10	10	12	110	10	120
	G	32.45	42.65**	18.34	0	0	3.63	97.07	85.84***	182.91***
*PGDH**	df	38	22	18	10	10	12	110	10	120
	G	60.17*	16.87	50.55***	41.88***	10.45	17.78	197.70***	131.84***	329.54***
*G3PDH-2**	df	19	11	9	5	5	6	55	5	60
	G	30.77*	20.45*	13.36	24.58***	5.18	17.28**	111.62***	95.97***	207.59***
*MPI**	df	76	44	36	20	20	24	220	20	240
	G	80.42	31.55	22.14	55.04***	25.48	19.38	234.01	254.73***	488.74***
*PGM-1**	df	19	11	9	5	5	6	55	5	60
	G	20.07	31.64***	25.88**	12.28*	2.33	34.74***	126.94***	140.11***	267.05***
*PGM-2**	df	38	22	18	10	10	12	110	10	120
	G	25.29	12.98	26.12	0	0	26.27**	90.66	39.47***	130.13
*sMDH-A1**	df	19	11	9	5	5	6	55	5	60
	G	30.97*	20.89*	10.31	22.37***	7.37	25.17***	117.08***	174.43***	291.51***
*sMDH-A2**	df	19	11	9	5	5	6	55	5	60
	G	51.18***	29.85**	12.57	8.39	2.83	12.08	116.90***	101.38***	218.28***
*sAAT-3**	df	38	22	18	10	10	12	110	10	120
	G	59.01*	18.69	67.20***	14.40	19.63*	28.37**	207.30***	314.96***	522.26***
*LDH-C**	df	19	11	9	5	5	6	55	5	60
	G	20.00	0	6.99	0	0	22.19**	49.18	49.56***	98.74**
*CK-B**	df	19	11	9	5	5	6	55	5	60
	G	11.87	6.76	0	13.37*	3.50	0	35.50	10.43	45.93
*TPI-1**	df	19	11	9	5	5	6	55	5	60
	G	0	0	15.41	0	0	0	15.41	19.77**	35.18

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APPENDIX 2. (*Concluded*)

Locus		Within Regions: South SE AK. Northern B.C.	Prince of Wales Is.	Central/ Northern SE	NW Queen Charlotte	SE Queen Charlotte Is.	Central BC	Total within	Total among	Total
*IDDH-2**	df	19	11	9	5	5	6	55	5	60
	G	5.55	6.74	5.65	6.32	3.39	7.12	34.77	2.81	37.58
*sMEP-1**	df	19	11	9	5	5	6	55	5	60
	G	18.31	7.11	0	0	0	2.58	28.00	6.07	34.07
*GPI-B1,2**	df	19	11	9	5	5	6	55	5	60
	G	10.50	0	6.29	0	3.40	0	20.19	6.61	26.80
*G3PDH-3**	df	19	11	9	5	5	6	55	5	60
	G	0	0	0	0	22.66***	0	22.66	42.90***	65.56
*TPI-4**	df	19	11	9	5	5	6	55	5	60
	G	18.14	0	0	3.26	0	9.23	30.63	12.85*	43.48
*FH**	df	38	22	18	10	10	12	110	10	120
	G	51.33	25.57	23.38	31.13***	12.98	7.70	152.09**	53.13***	205.22***
Total	df	893	517	423	235	235	282	2585	235	2820
	G	1000.29**	651.59***	592.12***	623.53***	224.96	639.45***	3731.94***	3842.30***	7714.35***

* = P <0.05, ** = P <0.01, *** = P <0.001.

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High-Biomass Forests of the Pacific Northwest: Who Manages Them and How Much is Protected?

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Abstract To examine ownership and protection status of forests with high-biomass stores (>200 Mg/ha) in the Pacific Northwest (PNW) region of the United States, we used the latest versions of publicly available datasets. Overlay, aggregation, and GIS-based computation of forest area in broad biomass classes in the PNW showed that the National Forests contained the largest area of high-biomass forests (48.4 % of regional total), but the area of high-biomass forest on private lands was important as well (22.8 %). Between 2000 and 2008, the loss of high-biomass forests to fire on the National Forests was 7.6 % (236,000 ha), while the loss of high-biomass forest to logging on private lands (364,000 ha) exceeded the losses to fire across all ownerships. Many remaining high-biomass forest stands are vulnerable to future harvest as only 20 % are strictly protected from logging, while 26 % are not protected at all. The level of protection for high-biomass forests varies by state, for example, 31 % of all high-biomass federal forests in Washington are in high-protection status compared to only 9 % in Oregon. Across the conterminous US, high-biomass forest covers <3 % of all forest land and the PNW region holds 56.8 % of this area or 5.87 million ha. Forests with high-biomass stores are important to document and monitor as they are scarce, often threatened by harvest and development, and their disturbance including timber harvest results in net C losses to the atmosphere that can take a new generation of trees many decades or centuries to offset.

Keywords Forest biomass · Forest management · Forest conservation · Carbon · Pacific Northwest

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Introduction

Forests are a critical part of the global biological carbon (C) cycle and can contribute to climate stabilization through uptake and storage of atmospheric C in live and dead trees and in soils (Nabuurs et al. 2007; Ryan et al. 2010). With increasing interest in incorporating forest C stores in forest management and climate change mitigation strategies, there is a growing need for improved understanding of spatial distribution of forest biomass across continents, regions, and landscapes. This is because biomass density (the quantity of biomass per unit area, or Mg dry weight per hectare) indicates the amount of C removed from the atmosphere and retained by vegetation and determines the amount of C that is emitted to the atmosphere (as CO_2, CO, and CH_4 through burning and decay) when ecosystems are disturbed (Houghton et al. 2009). The advances in forest monitoring using satellite imagery have been substantial over the past few decades and this technology is moving toward operational readiness for monitoring, reporting, and verification of forest cover, associated C stock, and their change over time (Goetz and Dubayah 2011). Mapping forest biomass has evolved into a major research priority and multiple methods have been proposed (e.g., Gonzalez et al. 2010; Lefsky 2010; Le Toan et al. 2011; Cartus et al. 2012). Biomass maps derived from

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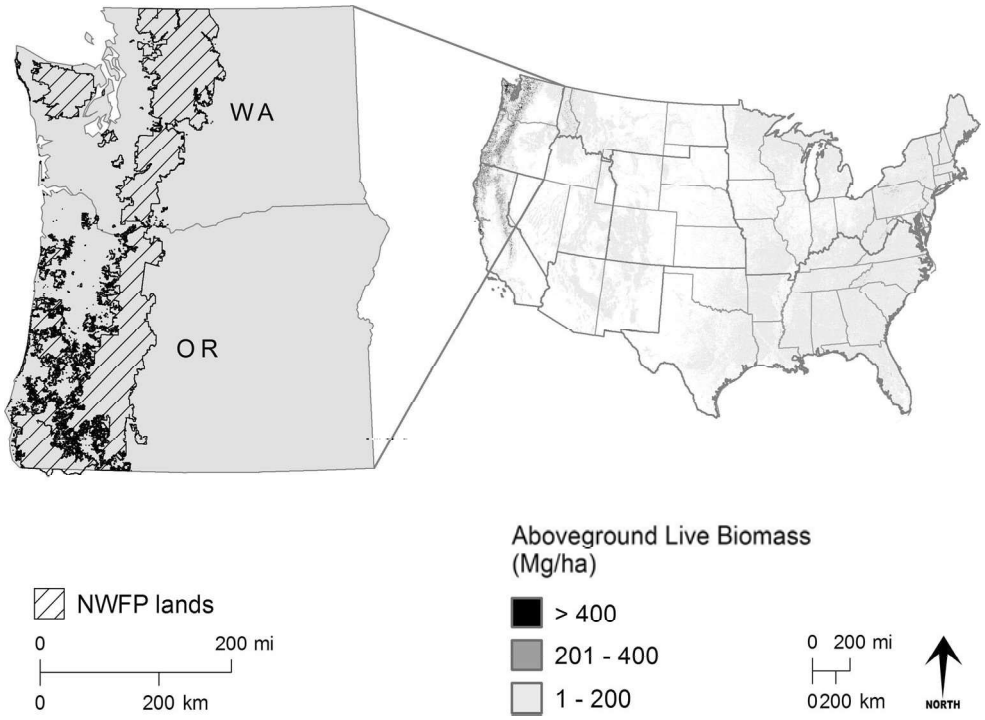

Fig. 1 Forest biomass classes across the conterminous United States as derived from the aggregated version of NBCD2000 dataset with location of study area in the Pacific Northwest and lands managed under Northwest Forest Plan

a combination of remote sensing and in situ data not only deliver transparent and current estimates of C stocks but also capture spatial variability necessary for prioritizing areas for conservation and other aspects of policy development and analysis. New remote sensing instruments aim to improve estimates of forest biomass across the globe at sufficient spatial resolution to inform climate change policies and to reduce uncertainty in regional to global scale C budgets (Goetz and Dubayah 2011). Yet, the bulk of policy analysis continues to rely on established forest inventories that deliver non-spatial estimates of forest biomass (e.g., Heath et al. 2011). Improved awareness of strengths and limitations of newly developed biomass maps is needed for effective use of these resources to inform policy development, implementation, and public scrutiny.

The impact of forest management practices on C exchange between forests and the atmosphere tends to increase in proportion to the amount of biomass C on site: while net losses of forest C to the atmosphere occur following any major forest disturbance, these losses are proportionally greater in high-biomass forests. Exceptional levels of C are stored in late-successional forests of the Pacific Northwest (PNW; Smithwick et al. 2002) and southeast Alaska (Leighty et al. 2006), and these forests are among the most C dense ecosystems in the world (Keith et al. 2009). The PNW forests contain substantial remnants of productive, high-biomass old-growth forests (Smithwick et al. 2002; Spies 2004; DellaSala 2011), whereas in other temperate regions these forests have been eliminated for centuries. Protecting biodiversity of late-successional forests was among the primary goals of the Northwest Forest Plan (NWFP) that shifted forest management on ~10 million ha of federal lands in the PNW from predominately timber extraction to ecosystem management and biodiversity conservation (Fig. 1; NWFP 2002; Mouer et al. 2005; DellaSala and Williams 2006). This change in management resulted in a considerable increase in C stores on federal forest lands within the first decade of plan implementation and this trend can be expected to continue into the future if the limits on timber harvest set under the NWFP are maintained (Krankina et al. 2012).

In the U.S., the national forest planning rule and national road map for responding to climate change require the Forest Service to conduct baseline C inventories so that C can be managed as a "multiple use" across the ~80 million ha national forest system (USDA Forest Service 2010; 2012). Monitoring forest C stores is also integral to the development of an emerging C market for private forest lands (e.g., Alig et al. 2010; California Climate Action Registry www.climateregistry.org/ accessed December 17, 2007). The largest national ground-based dataset was developed by the USDA Forest Inventory and Analysis (FIA) Program and used extensively in studies of forest biomass at national, regional, and state levels (Smith 2002; Heath et al. 2011). Summaries of plot data are available at county level (Van Deusen and Heath 2010), but the sampling method is designed to produce averages for large areas rather than characterizing spatial distribution at fine

Table 1 Area estimates of forest biomass classes and disturbances by land ownership class in Oregon and Washington States combined (thousand ha)

Ownership class	Forest area in biomass classes[a]				Forest area disturbed from 2000 to 2008		High-biomass[b] forest area disturbed from 2000 to 2008		Total forest area[c]	Total land area
	Low (1–200 Mg/ha)	High (201–400 Mg/ha)	Very high (>400 Mg/ha)		Fire	Other disturbance	Fire	Other disturbance		
USFS	3,784	2,121	716		628	246	236	35	7,495	10,003
NPS	131	265	156		6	1	4	1	560	865
BLM	288	343	152		26	94	8	48	902	6,511
Other Public	1,149	597	179		51	151	7	69	2,125	5,101
Private	3,108	1,174	163		58	557	6	364	5,061	19,936
Total	**8,459**	**4,499**	**1,366**		**769**	**1,049**	**261**	**518**	**16,142**	**42,416**

[a] Excluding 2000–2008 disturbance

[b] >200 Mg/ha

[c] In year 2000

resolutions needed for local management decisions. The FIA dataset was used in combination with remotely sensed data to map forest biomass across the conterminous USA at 240 m resolution (Blackard et al. 2008) and at 30-m resolution (National Biomass and Carbon Dataset for the year 2000 (NBCD2000); http://www.whrc.org/mapping/nbcd/index.html, accessed November 21, 2012; Kellndorfer et al. 2006, 2013). Both datasets are freely available to the public.

Our objective was to develop and demonstrate a simple method for using the NBCD2000 dataset to map forests with high-biomass stores in the PNW, examine their ownership and protection status, and assess the area of different types of disturbance affecting high-biomass forests between 2000 and 2008. The overall purpose was to provide an example of using newly available spatial datasets to answer some common questions of forest conservation.

Study Area and Methods

The study area encompasses 42.4 million ha in two states, Oregon (OR) and Washington (WA), that together form the Forest Service's Pacific Northwest Region (Fig. 1; Table 1). Within this region, we examined the area covered by the NWFP and its land-use allocations in greater detail. The overall approach relies on using the latest versions of publicly available spatial datasets for overlay, aggregation, and GIS-based computation of forest area in broad biomass classes across a range of categories that characterize ownership, land-use allocations, disturbance, and protection status of forest lands.

The primary source of data for mapping forest biomass classes was the NBCD2000 dataset (Kellndorfer et al. 2006, 2013). The dataset represents live aboveground biomass of trees with >5 in (12.7 cm) diameter at breast height (DBH) in 30 m pixels. Biomass values in NBCD2000 dataset were predicted using statistical fusion of several data sources, including high-resolution InSAR data acquired from the 2000 Shuttle Radar Topography Mission (SRTM); optical remote sensing data from the Landsat ETM+ sensor (three seasons); USGS National Land Cover Dataset 2001 (NLCD 2001); LANDFIRE (existing vegetation type; USGS 2011); USGS National Elevation Dataset; and USDA FIA data (Kellndorfer et al. 2006; 2013). The biomass values were estimated for each pixel and then averaged at a "stand" patch level (~2 ha average). The standard error of biomass values based on bootstrap validation with USDA FIA plot data is ±139 Mg/ha.

We used the values from NBCD2000 dataset within the PNW study region to assign the 30-m pixels to four biomass classes: <1 Mg/ha (labeled non-forest), 1–200 Mg/ha

(Low Biomass), 201–400 Mg/ha (High Biomass), and >400 Mg/ha (very high biomass). We chose these broad biomass classes because of the high-estimated standard error of the source biomass dataset. Classification breaks were chosen to separate the total forest area into comparable parts with all biomass classes represented within each ownership class. Furthermore, 200 Mg/ha in aboveground live tree biomass approximates the biomass store common for harvest-age productive Douglas-fir (*Pseudotsuga menziesii*) stands (Krankina et al. 2012), the regional average of inventory plots on USDA FS forestlands (Heath et al. 2011), and the lower range of biomass in old-growth forests, while 400 Mg/ha approximates the mid-range for old-growth stands (Smithwick et al. 2002; Keith et al. 2009). In addition to the primary 30-m resolution NBCD2000 dataset, we also used an aggregated version of this dataset at 240-m resolution (http://www.whrc.org/mapping/nbcd/index.html; accessed November 21, 2012) to characterize the share of PNW high-biomass forest area in the nationwide total (Fig. 1; Online Resource 2).

Because NBCD2000 reflects the distribution of biomass circa year 2000, we updated our biomass class map by removing all pixels identified as disturbed in LANDFIRE 2008 dataset (http://landfire.cr.usgs.gov/viewer/; accessed August 31, 2012; and obtained on DVD from Heather Kreilick hkreilick@usgs.gov). The Vegetation Disturbance layer for 1999–2008 provides spatial information on vegetation transitions at 30-m resolution, including disturbance year, type, and severity of disturbance derived mainly from Landsat TM/ETM and MODIS data (Vogelmann et al. 2011; USGS 2012). To characterize the impact of disturbance on high-biomass forests, we computed the disturbed area by biomass class with separation of "fire" from other disturbance types that were examined in aggregate (Table 1). This update of our biomass class map accounts for losses of high-biomass forest to various kinds of disturbance but does not reflect recruitment of high-biomass forests with tree growth over time. We acknowledge this bias but could not eliminate it as the required spatial data are not readily available.

USDA FIA plot-level biomass data were used to assess the accuracy of our updated biomass class map, i.e., the agreement of field-based estimates of forest biomass from FIA plots with assignment of corresponding map pixels to biomass classes. The FIA plot data are publically available (http://www.fia.fs.fed.us/tools-data/, accessed December 5, 2013) with the exception of precise plot location coordinates. FIA staff has unrestricted access to the plot location coordinates and the co-author who is a FIA staff member (Mikhail Yatskov) used plot coordinates to identify mapped biomass class for each FIA plot. This was the only step that relied on data not publicly available.

Forest inventory plots are distributed across all ownerships on a hexagonal grid with one plot being roughly representative of 2,400 ha of land area (Bechtold and Patterson 2005). Plots are re-measured on 10-year cycles to track the land-use change over time as well as changes in biomass, plant species composition, parameters associated with disturbances, and other factors represented by more than 300 collected variables (Smith 2002). Our FIA dataset included 11,887 plots measured during a 10-year cycle that started in 2001. For the reference dataset, we selected a subset of 3,339 plots that were not disturbed since last inventory cycle and were measured between 2008 and 2010. The latter criterion was added to make sure that plot measurements used in our accuracy assessment were not among those used to develop the NBCD2000 dataset (Kellndorfer et al. 2006; 2013) and to minimize the time difference between FIA plot measurements in the field and the biomass class map which was updated to year 2008. We then removed from our reference dataset the plots that were not measured in the field and plots where the proportion of forest cover was <90 % to eliminate plot observations with ambiguous attribution to a specific biomass class. The resulting dataset included 2,898 plots; in each of them live aboveground biomass (Mg/ha) for trees >12.7 cm DBH was estimated from field measurements using regional biomass equations (Zhou and Hemstrom 2010). These estimates were assigned to circles with a radius of 56.4 m (1 ha area) that were overlaid with our updated biomass class map using ArcGIS 10.1. For each circle, we calculated the area that belonged to different classes on our biomass map. The circles where the majority biomass class occupied <90 % of the total area were dropped from the set and the remaining 2,226 plots were used to evaluate the performance of the biomass class map. We constructed a confusion matrix and calculated accuracy metrics, including the error of omission (exclusion) and commission (inclusion) for each class, the overall agreement, and chance-corrected agreement (Kappa, Cohen 1960; See Online Resource 1 for details).

To characterize the current protection status and ownership of high-biomass forests, we used the Protected Areas Database of the United States (PADUS), version 1.2. (US Geological Survey, Gap Analysis Program (GAP), http://gapanalysis.usgs.gov/padus/download/, accessed November 21, 2012). PAD-US is an inventory of marine and terrestrial protected areas that are defined as being dedicated to the preservation of biological diversity and to other natural, recreation ,and cultural uses, managed for these purposes through legal or other effective means (National Gap Analysis Program 2011). For our analysis, we examined two sets of variables: GAP Status Code (values range from 1 to 4 in decreasing levels of protection) and Ownership class that included National Park Service (NPS), US Forest Service (USFS), Bureau of Land Management (BLM), and Other Public (including other federal, state, country, and Native

Table 2 Forest area and biomass classes on Northwest Forest Plan land allocations within Oregon and Washington (thousand ha)

State	NWFP Land-use allocation[a]	Total land area	Forest area (≥1 Mg/ha)	High-biomass forest area[b]		
				Total	IRA[c]	GAP 1 and 2 status
Oregon	AW/CR	854.2	704.5	361.6	39.3	256.3
	LSR	1,383.8	1,123.8	740.1	103.4	34.7
	Matrix	1,675.3	1,343.9	817.1	34.3	2.0
	State total	3,913.4	3,172.2	1,918.8	177.0	293.1
Washington	AW/CR	1,880.6	1,219.9	828.0	39.7	760.5
	LSR	976.5	802.5	566.4	220.9	22.2
	Matrix	720.1	516.5	295.4	58.5	6.5
	State total	3,577.4	2,538.9	1,689.8	319.0	789.2
Grand total		7,490.8	5,711.1	3,608.6	496.1	1,082.2

[a] Administratively Withdrawn/Congressionally Reserved (AW/CR); late-successional reserves (LSR); after Mouer et al. (2005)

[b] >200 Mg/ha; high biomass and very high biomass classes combined

[c] Inventoried roadless areas

American lands). We assumed that lands not classified into these four categories were Private. In addition, we examined overlap between high-biomass forests and Inventoried Roadless Areas (IRA; http://sagemap.wr.usgs.gov/ftp/unitedstates/USFS/ira_us_dd.htm, accessed November 21, 2012) to determine how well this administrative category can contribute to protection of high-biomass forests in our study area. The intent of the 2001 roadless area conservation rule is to provide lasting protection for these roadless areas in the context of multiple-use management, primarily for the purpose of "watershed and ecosystem health" (USDA Forest Service 2000). Most of these areas are concentrated in the western United States and Alaska. Finally, we examined the extent of high-biomass forests within the NWFP land-use allocations (http://www.reo.gov/gis/data/gisdata/index.htm, accessed June 13, 2012). The NWFP record of decision divided federal land into seven land-use allocations of varying levels of protection; Mouer et al. (2005) combined or further split some allocations and we used these generalized land-use categories for our study area (Table 2).

To characterize the current protection status of high-biomass forests, we used polygon data on ownership, disturbance (between 2000 and 2008), land management allocations, and protection status as masks in the Spatial Analyst Toolbox within ArcGIS 10.1 to extract the biomass class map for each land category of interest. We then computed the area of biomass classes using Zonal Statistics tool in the Spatial Analyst Toolbox.

Results

The assessment of accuracy of our biomass class map with ground measurements on FIA plots indicated that 85.8 % of plots in our sample were mapped correctly with a Kappa value of 65.9 % (Online Resource 1). A large portion of FIA plots with biomass values close to the lower limit of

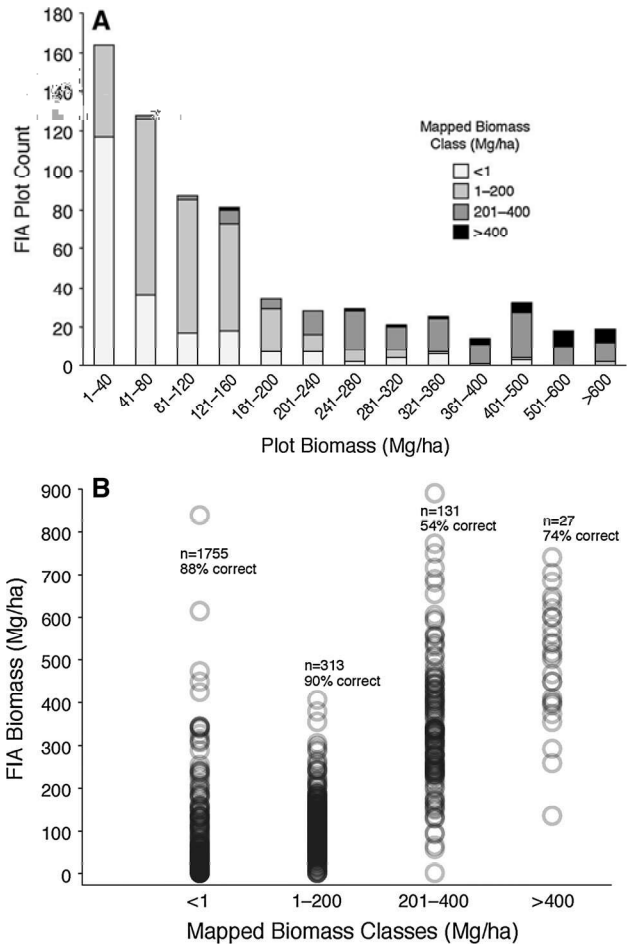

Fig. 2 Agreement between NBCD2000 dataset and biomass estimates for FIA plots in the Pacific Northwest study area: **a** FIA plot counts by mapped biomass classes and **b** distribution of forest biomass values in FIA plots across mapped biomass classes in NBCD2000 dataset

Low-Biomass Class were mapped as non-forest (assigned biomass values <1 Mg/ha in NBCD2000 dataset): among plots with field-based biomass estimates of 1–40 Mg/ha, 77 % were incorrectly assigned to <1 Mg/ha class, while

among the plots with biomass ranging from 80 to 200 Mg/ha <25 % were similarly misclassified (Fig. 2a). For the high-biomass class (201–400 Mg/ha), omission and commission errors were well balanced, but in the very high-biomass Class (>400 Mg/ha), the error of omission (71 %) was greater than that of commission (25.9 %, Online Resource 1); in other words—the Very High-Biomass Class (>400 Mg/ha) was under-reported in our biomass class map. The distribution of plot-level biomass values by mapped biomass class demonstrates the degree of biomass class separation and confusion (Fig. 2b). Because of significant confusion between the two high-biomass classes, we opted to report most results for the combined high-biomass class (>200 Mg/ha). Within the combined high-biomass class, 88.6 % of FIA plots were classified correctly and the overall accuracy of three-class biomass map was higher—88.0 %, Kappa 71.0 % (Online Resource 1). Where the results for the very high-biomass class are reported, they likely reflect under-estimation of the area for this class and may have lower overall accuracy.

The total area of mapped forest cover in our PNW study area is 16.1 million ha (Table 1, Online Resource 3) which is generally consistent but lower than the forest area estimate for OR and WA reported by Smith et al. (2001): 51,612000 acres or 20.9 million ha. The definition of forest cover used in this study (≥1 Mg/ha aboveground live tree biomass) is different from definition adopted in the FIA program (Smith et al. 2001); therefore, these area estimates are not directly comparable. The map-based estimate of forest cover excluded forest area disturbed from 2000 to 2008; this combined with the inclusion of lands without tree cover within FIA definition of forest likely accounts for most of the difference in estimates.

High-Biomass Forests Distribution and Losses—Total forest area that was disturbed from 2000 to 2008 was 1.82 million ha or 1.25 % per year on average. With disturbed forest area excluded, high-biomass (>200 Mg/ha) forest area was 5.87 million ha or 41 % of the total forest area, while very high-biomass forests occupied 1.37 million ha or 10 % (Table 1). These high-biomass forests represent a large proportion of all high-biomass forests nation wide (Fig. 1; Online Resource 2). The aggregated version of NBCD2000 used at the national scale suggests that within the conterminous United States, the PNW region holds 56.8 % of forest area with biomass >200 Mg/ha and as much as 77.2 % of forest area with biomass >400 Mg/ha. The coarser resolution of the national dataset (240 m) may have resulted in omission of high-biomass forests where they occur in dispersed small patches and this hampers comparison of high-biomass forest areas in different parts of the country. However, the scarcity of high-biomass forests and their extreme overall concentration in western United States is evident: high-biomass forest occupies <3 % of all forest land in conterminous US, and the PNW and Pacific Southwest regions combined hold 89 % of those forests (Fig. 1; Online Resource 2).

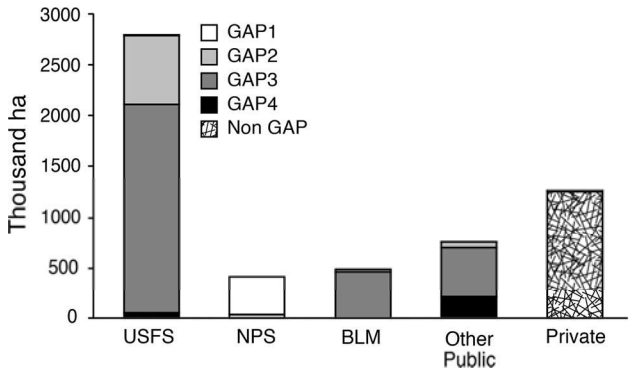

Fig. 3 High-biomass (>200 Mg/ha) forest area distribution by ownership and GAP status for the Pacific Northwest study area

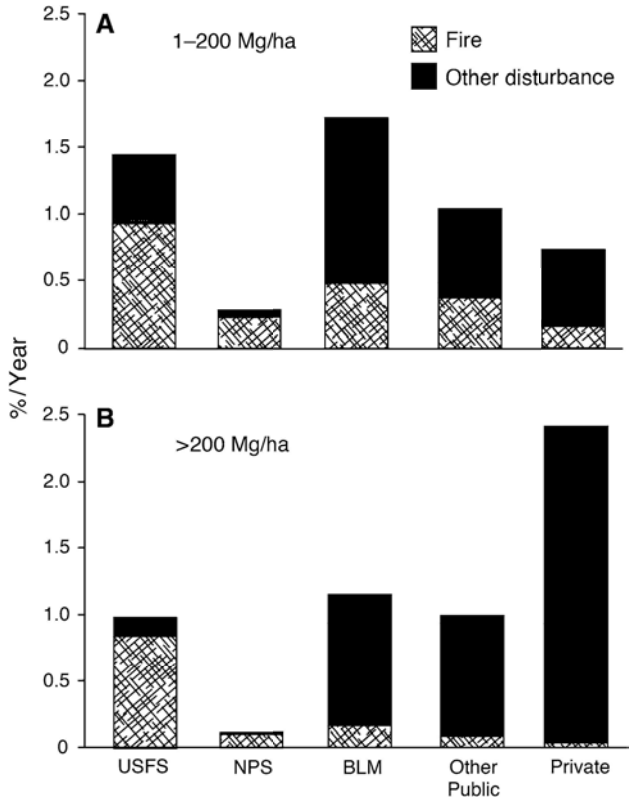

Fig. 4 Average annual disturbance rates for forests in the Pacific Northwest study area between 2000 and 2008: **a** low-biomass forests; **b** high-biomass forests

Among ownership types in the PNW, USFS lands (primarily National Forests) contained the largest area of high-biomass forests (48.4 % of regional total), but private lands contained a significant portion of high-biomass forest as well (22.8 %; Table 1; Fig. 3). More than half of very

high-biomass area was on USFS lands, while the share of other four ownership classes was 11–13 % in each. As a fraction of total forest area in an ownership class, the proportion of high-biomass forest area was the largest on NPS and BLM lands (76.6 and 68.1 %, respectively), while on private lands, the proportion of high-biomass forest was relatively low (38.6 %) with only 3.7 % in >400 Mg/ha class (Table 1; Fig. 3).

On NPS land, the proportion of forest area disturbed by all factors between 2000 and 2008 was only 0.16 % per year on average, other ownership classes had much higher disturbance rates (Fig. 4). On USFS lands, fire was the dominant disturbance factor, while other types of disturbance played a much greater role in all other ownerships. The loss of high-biomass forest stands to disturbance both in terms of total area (Table 1) and as a proportion of area in 2000 (Fig. 4) was smaller than the loss of low-biomass forest area with one important exception: on private lands, the loss of high-biomass forest was four times greater than low-biomass forests. The loss of private high-biomass forests between 2000 and 2008 was 21.3 % (364,000 ha) and was mostly associated with non-fire disturbance (primarily logging). The loss of high-biomass forests to fire on USFS lands was 7.6 % of their area in year 2000 (236,000 ha). Overall, the area of high-biomass forest logged on private lands exceeded the total area burned across all ownerships (Table 1). Among public ownerships, the rate of forest loss was greatest on BLM lands (1.25 % per year in high-biomass forest; Fig. 4), mostly to non-fire disturbance (logging). Across all ownerships, the average annual rate of disturbance of high-biomass forest was 1.32 % with fire responsible for about one-third of this loss.

Protection Status of High-Biomass Forests in the PNW—NWFP lands in OR and WA contained 3.6 million ha of high-biomass forest or 61.5 % of the regional total (Table 2). This area was somewhat greater in OR than in WA, but high-biomass area within IRAs and in high-protection GAP status (Gap 1 and 2) was much greater in WA. For example, 31 % of all high-biomass forest lands in WA were in high-protection GAP status compared to only 9 % in OR. Fire was the primary disturbance factor within NWFP lands and fire losses of high-biomass forest between 2000 and 2008 totaled 217,000 ha, while all other factors combined accounted for 74,000 ha loss. However, the average rate of high-biomass forest loss to disturbance on NWFP lands was 0.83 % per year—lower than 2.37 % per year on private lands or 1.32 % per year regional average rate (Fig. 4).

IRAs contained 496,000 ha or 17.5 % of all high-biomass forest lands in USFS ownership in our study area (Table 2) and 132,000 ha or 18.4 % of very high-biomass forests. GAP status information was available only for public lands and primarily reflected the ownership status of high-biomass forests (Fig. 3). High-biomass forest lands with GAP1 status were concentrated on NPS lands, while GAP2 and three occurred mainly on USFS forest lands (with GAP3 prevailing). On other public ownerships, high-biomass forests were in GAP3 and four status (Fig. 3). Across all ownerships, only 20 % of high-biomass forest had strict protection from logging under GAP 1 or 2 status, while 26 % were in GAP4 or no-GAP status receiving little to no protection.

Discussion

The mapping of forest biomass has improved greatly in past decades with increasing use of satellite and aircraft remote sensing. NBCD2000 dataset appears to represent the full range of biomass values better than the Blackard et al. (2008) dataset, where over-estimation of low biomass values and under-estimation of high biomass were reported. Conversely, NBCD2000 assigned biomass values <1 Mg/ha to majority of pixels that coincide with FIA plots with biomass ranging from 1 to 40 Mg/ha; thus under-reporting the area of forest with low-biomass (Fig. 2). For stands with very high-biomass, NBCD2000 tends to under-estimate biomass (Online Resource 1; Fig. 2).

The accuracy metrics in our analysis indicate a moderate level of agreement between the updated biomass class map (Online Resource 3) and the reference data (85.6 % overall agreement for 4-class biomass map, 88.0 % with High Biomass and very high biomass classes combined; Online Resource 3). This suggests that the aggregation of pixel-level biomass values into broad classes served to mitigate the problem of high error in the source NBCD2000 dataset and the map can be considered robust. Yet, at the pixel or stand level, the accuracy of large-area datasets remains inadequate for effective operational monitoring of C stocks (Houghton et al. 2009; Goetz and Dubayah 2011). In the future, the combined use of passive optical remote sensing with light detection and ranging (LiDAR) instruments and the new generation of radar sensors is widely expected to improve the accuracy of biomass maps and meet the needs of forest C monitoring (Gonzalez et al. 2010; Lefsky 2010; Le Toan et al. 2011; Goetz and Dubayah 2011). Nevertheless, currently available biomass maps can provide useful information on patterns of spatial distribution and abundance or scarcity of high-biomass forests over large areas and their losses due to disturbance (Fig. 1; Online Resource 2, 3). Combined with data on land-use designations and protection status of forest lands, the available biomass maps can help assess the ownership status and the extent to which high-biomass forests are protected versus those vulnerable to future harvests.

Our results are broadly consistent with earlier studies that used remote sensing methods to assess the area of mature, old-growth, and large-diameter forests (LDF) in the PNW and their loss to disturbance (Strittholt et al. 2006; Healey et al. 2008). However, the focus on biomass rather than stand age (Strittholt et al. 2006) or stand structure (Healey et al. 2008) makes our results more relevant to planning C management in forest ecosystems as part of climate change mitigation policies (USDA Forest Service 2010, 2012). It is also a likely reason for differences in results. For example, Strittholt et al. (2006) report that 26 % of old-growth forest were strictly protected (GAP1 and GAP2), whereas only 20 % of high-biomass forest were similarly protected (Tables 1, 2; Fig. 3). Furthermore, the loss of LDF across all ownerships during the period following implementation of the NWFP was reported by Healey et al. (2008) at 0.73 % annually, whereas our estimate of high-biomass forest loss to disturbance was nearly twice as high (1.32 % per year), primarily because of logging on private lands. Thinning has become a major type of logging on NWFP lands, and thinned stands were presumed to retain their LDF status (Healey et al. 2008) but thinning significantly reduces forest biomass store. Clearly, the NWFP offers less protection for high-biomass forests compared to LDF or old growth, especially for the most productive stands that can reach 200 Mg/ha biomass level when they are relatively young (~40 years old). Protecting high-biomass forest may be a greater challenge as it presents a more direct conflict with economic gains from timber harvest than protection of old growth, especially old growth with relatively low biomass stores.

While the biomass maps used in this analysis have been available to the public for some time, to our knowledge they have not been used for a quantitative assessment of the area of high-biomass forests and their protection status. The development of approaches and methods for spatial data analysis, like the one presented here, is needed so that forest managers and interest groups can extract pertinent information from available biomass maps. The established FIA sampling methods and analysis tools target broad-scale averages (Van Deusen and Heath 2010; Heath et al. 2011) and cannot deliver adequate characterization of the spatial distribution of forests across the range of biomass values. Forests with high-biomass stores are important to document as they are scarce (Fig. 1, Online Resource 2) and often threatened by harvest and development. The disturbance of high-biomass forests especially timber harvest results in net C losses to the atmosphere that can take a new generation of trees many decades or centuries to offset (e.g., Houghton et al. 2009; Krankina et al. 2012). Yet, protection of high-biomass forests and their C stocks is not among options for managing C on forest lands proposed by the national road map for responding to climate change (USDA Forest Service 2010), the Pacific Coast Action Plan on Climate and Energy (http://www.pacificcoastcollaborative.org/Documents/Pacific%20Coast%20Climate%20Action%20Plan.pdf, accessed December 9, 2013), or The President's Climate Action Plan (http://www.whitehouse.gov/sites/default/files/image/president27sclimateactionplan.pdf, accessed December 9, 2013). Our biomass class map (Online Resource 3) can help identify critical gaps in protection of high-biomass forests in the PNW, better target future conservation programs related to C stores and climate change mitigation efforts, and support the inclusion of high-biomass forest protection in the set of climate change mitigation options on forest lands.

Availability of data on spatial distribution of high-biomass forests could have improved the effectiveness of forest conservation under the NWFP. The NWFP was an important step forward in protecting late-successional habitat for threatened species (e.g., Mouer et al. 2005; DellaSala and Williams 2006) and, as a side benefit, resulted in active C sequestration on federal forest lands (Turner et al. 2011; Krankina et al. 2012). However, there is a surprising discrepancy in protection level of high-biomass forests in OR and WA and overall limited protection from harvest (GAP3, GAP4 or no-GAP) for ~70 % of high-biomass forests managed under NWFP (Table 2). Among publicly owned forest lands, BLM has the highest concentration of high-biomass forests (Fig. 3), which were harvested at a higher rate compared to other public ownerships in 2000–2008 (Fig. 4). Many of the remaining high-biomass forests on BLM lands are designated for logging under recent proposals for expanded timber harvest on NWFP lands (e.g., DeFazio et al. 2012; Wyden 2013).

The vulnerability of old-growth forest to wildland fire on USFS lands has dominated the debate on future conservation strategies in the PNW (Spies et al. 2006; DellaSala and Williams 2006; Healey et al. 2008). This debate largely overlooked the impact of ongoing logging on public lands, yet logging accounts for a greater loss of high-biomass forest than fire on BLM lands and in the other public lands category that includes state and tribal forests (Table 1; Fig. 4). While not all harvested high-biomass forests are old growth, this continued harvest on public lands depletes the cohort of stands where old-growth characteristics can develop over time. In addition, fire and other natural disturbances in high-biomass forests transfer C from live biomass into dead biomass pool, but the total C store on site remains high, while logging moves C off-site leaving a greatly reduced total C store on forest land (Krankina and Harmon 2006).

Significant portions of high-biomass forests in the PNW that are vulnerable to additional losses are privately owned (Fig. 3). The biomass class map can help identify areas

where privately owned high-biomass forests are concentrated and where targeted conservation incentives for private owners may be effective in protecting the diverse ecosystem services provided by high-biomass forests, especially long-term C storage (Foley et al. 2009). Studies of the effect of C price on private forest owner behavior in Western OR showed that even at a low C price some extension of harvest rotation can be expected (Im et al. 2007; Alig et al. 2010). In addition to slowing the losses of high-biomass forests and reducing associated C emissions, significant net sequestration of C can be expected from postponing harvest of relatively young and productive high-biomass forests on private lands (Krankina and Harmon 2006; Foley et al. 2009; Ryan et al. 2010). The incentives to postpone harvest can also help inform stakeholder's importance of protecting high-carbon forests for purposes of climate change mitigation.

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Yellow-cedar: climate change and natural history at odds

A slow race is unfolding on the British Columbian and southeast Alaskan coast. The race involves Alaska yellow-cedar (*Callitropsis nootkatensis*), an ecologically, culturally, and economically important tree species that is uniquely susceptible to climate change due to its natural history and ecological strategies. In the southern and coastal portions of its range, yellow-cedar is dying rapidly due to a warming climate; massive cedar mortality (observed in an area > 200 000 ha; Figure 1) has occurred and continues to occur. At the same time, on the edge of its northern range, this species is slowly expanding into suitable habitat and more favorable climes, with no major barriers to northern expansion immediately in sight. As the climate continues to warm, the forest as a whole could look very different, depending on how this race between southern range contraction and northern range expansion proceeds.

Yellow-cedar is a member of the cypress family (Cupressaceae), an ancient group that contains the tallest (coast redwood), largest (sequoia), and second oldest (Alerce) trees on the planet. Extant members are found in a variety of habitats on every continent except Antarctica (with likely fossil evidence there). Yellow-cedar apparently speciated relatively late, splitting from the junipers 50–75 million years ago, then dispersing to North America from Asia (Mao *et al.* 2012). It is one of the slowest growing conifers in the Pacific Northwest, and most at home in sparsely treed, boggy sites (known as muskegs) with poorly drained soils and little competition for light. Yellow-cedar invests a substantial amount of energy into defensive (including antifungal) compounds, giving it surprising durability despite the extremely wet, nearly saturated conditions where it grows – characteristics that preclude the occurrence of most other tree species. The wood has been used for millennia by Alaskan and British Columbian Native peoples, as building material and to make canoes, and is still prized for outdoor furniture and framing. Fallen limbs and whole trees retain their distinctive chemistry for decades after death, producing unusually long-lasting debris on the wet forest floor (Kelsey *et al.* 2005).

Specialization in muskegs and other poorly drained soils is the key to yellow-cedar's success. Nitrogen (N) limitation is common throughout the temperate zones, and is exacerbated further by wet soils. Like most of the Cupressaceae, yellow-cedar preferentially takes up nitrate (NO_3^-), which is produced in the shallow, unsaturated upper few centimeters of the soil profile (Krajina *et al.* 1973); however, internal electrochemical charges associated with this type of nutrient uptake must be balanced in some fashion. One way to achieve this balance is to take in calcium (Ca_2^+) – yellow-cedar accumulates this nutrient far above its metabolic needs, after which the calcium is transported to the foliage and, ultimately, into the upper layers of soil as detritus from "foliage rain". This results in an advantageous, self-promoting positive feedback as increased soil pH (from the increased calcium concentration) promotes nitrification, increasing N availability in the shallow upper portions of these slowly cycling soils (D'Amore *et al.* 2009). A second pulse of nitrification occurs briefly in the spring, as microbial cells in the soil burst during rapid freeze–thaw cycles. The ability to take advantage of this surge in available N requires an aggressive, but potentially risky, growth strategy. Yellow-cedar becomes photosynthetically active earlier in the spring than the other tree species in the region, an opportunistic response to this temporally limited, shallow N pool (D'Amore *et al.* 2009). During these times, yellow-cedar remains photosynthetically active at low air temperatures, even slightly below freezing (Schaberg *et al.* 2011). Overall, these strategies are well-suited for cool, wet, N-limited landscapes.

Unfortunately, specialization may result in dependency on a narrow range of environmental conditions, and vulnerability when those conditions change. In the case of yellow-cedar, both shallow rooting (due to water-logged soils and the need to exploit shallow N sources) and physiological adaptations for early-spring growth expose trees to potential freezing injury should soil temperatures dip too low (Schaberg *et al.* 2011). This isn't a problem if there is an ample snowpack that lingers late into spring, as the area beneath the snow is buffered from cold air temperatures until long after the threat of a deep freeze is past (incidentally, late snowpack also protects seedlings from Sitka and Columbian black-tailed deer [*Odocoileus hemionus sitkensis* and *O h columbianus*], which appear to target cedar for winter browse). As average temperatures have risen following the Little Ice Age (which ended during the mid-19th century CE), and more rapidly with anthropogenic atmospheric carbon dioxide accumulation, rain has replaced snow throughout much of the year, reducing that insulating blanket of snow in late spring (Hennon *et al.* 2012). Consequently, yellow-cedars are out of sync with their temperature environment, and their roots – shallow and physiologically active – become exposed to spring freezing events (when they do succeed in better drained soils, it is because their roots are deeper). It doesn't take much to cause root mortality; soil temperatures of –5°C are low enough. If a sufficient number of roots are killed in one year, or over a few successive years, the entire tree dies. Because of this, wide swaths of dead cedars extend across southeast Alaska and into neighboring British Columbia (Figure 1a), with mortality rates higher than 70% in some areas (Hennon *et al.* 2012).

Leave the heart of concentrated cedar mortality and

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travel a couple of hours northeast by float plane, or a bit longer by boat, and the situation looks quite different. Slightly colder average temperatures translate into more snow, and a snowpack that lingers longer. The same spruce–hemlock (*Picea–Tsuga*) forests dominate as in the south, with muskegs interspersed wherever the slope evens out or bedrock cups runoff into wet pockets. Yet yellow-cedar is rarely seen here, and most people don't even know it's there. It's not entirely absent – small, isolated groups are scattered about, seemingly at random. Some spots have upwards of 40 mature giants, others five, and in one case, a lonely cedar stands all by itself alongside an old mining ditch (Figure 1b). This is the leading edge of the other part of the race, the race into suitable habitat. These cedars appear to be new arrivals at the leading edge of an ongoing, slow migration from beyond the southern end of the Cordilleran Ice Sheet during the Last Glacial Maximum, hypothesized glacial refugia along the outer coast of southeast Alaska and Queen Charlotte Islands (Carrara *et al.* 2007), or both.

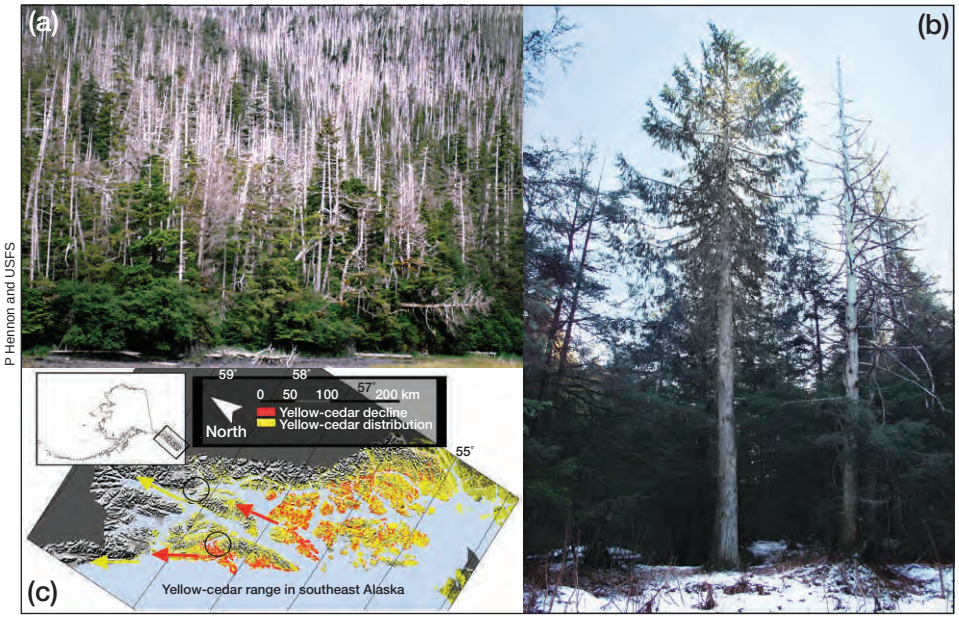

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Figure 1. *Yellow-cedar (*Callitropsis nootkatensis*) decline/expansion and map of general region. (a) Hillside near Sitka, Alaska, dominated by dead and dying yellow-cedar (with some residual spruce [*Picea*]) from freezing mortality as a result of shallow rooting and low snowpack. (b) On the other side of the species' climatic range, range-edge populations are slowly spreading north. The "lonely cedar" growing near Douglas, Alaska, is shown (coring evidence indicates that the tree sprouted in the year 1891). No other individuals are known within several kilometers. (c) A map of yellow-cedar distribution and decline in southeast Alaska, with the picture locations (circles) and migration/decline advance (arrows).*

Yellow-cedar is again suffering because of its biology, however; a number of factors combine to keep its migration at a near-glacial pace. Only about one-quarter of its seeds are viable, and they tend to be heavy; this likely enables them to establish on thicker organic soils, but also limits their estimated dispersal distance to under 120 m (Burns and Honkala 1990). In an archipelago environment where muskegs, although plentiful, are scattered, dispersal is a slow and jerky affair. Chance long-distance dispersal, when it occurs, is probably a product of strong fall and winter winds from the south, concurrent with the release of viable seed crops. Some of these seeds may make it to muskeg sites, establishing a new population, and pushing the range edge that much farther. Layering (asexual reproduction) is fairly common in muskegs, and this may serve to fill in a stand after a successful long-distance dispersal event, though slowly (Hennon *et al.* 2012). Forest blowdown may also provide germination sites, allowing for the occasional establishment of yellow-cedar in drier upland locations. We know relatively little about yellow-cedar's spread; for instance, how do these pioneers interact with preexisting plant communities? Many questions remain regarding dispersal and establishment along the leading range edge, which are key in predicting the ultimate impacts of climate change on the species.

Standing at that advancing edge today, though, things look healthy. The scattered yellow-cedar populations appear to be new and growing – there are few dead individuals, and ample regeneration. But climate models make it clear that the current snowpacks that maintain favorable environmental conditions are quickly diminishing (Shanley *et al.* 2015). Topography will offer some respite, as sheltered and high-elevation areas will retain snow, and for now well-drained soils appear to protect cedar from the cold. Nonetheless, available habitat will certainly be drastically reduced. This is where humans are considering joining the race, potentially implementing policies of assisted migration and conserving yellow-cedar in safe sites remaining across its range, such as high-elevation locations or pockets where snow lingers due to cold air drainage. Experimental plantings by the US Forest Service near the northern range edge grow well, and land managers are considering further aiding this species in its slow march north. For now, at least, the race is on.

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Please see WebReferences

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