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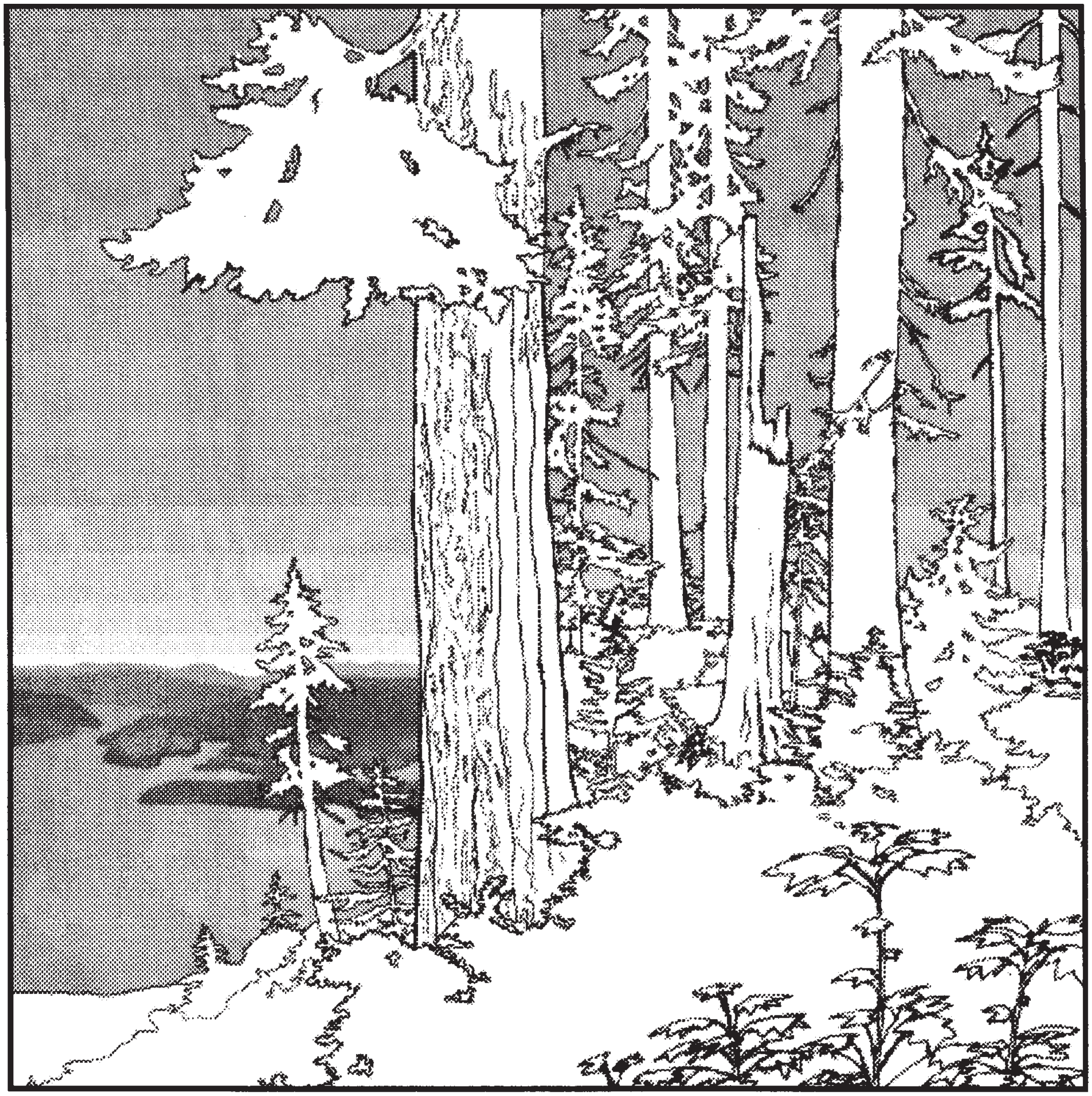
The Alexander Archipelago Wolf: A Conservation Assessment

David K. Person, Matthew Kirchhoff,
Victor Van Ballenberghe, George C. Iverson,
and Edward Grossman



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Conservation and Resource Assessments for the Tongass Land Management Plan Revision

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Abstract

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We summarized the scientific information available for the Alexander Archipelago wolf (*Canis lupus ligoni*) in the Tongass National Forest of southeast Alaska. Information concerning the morphology, distribution, taxonomy, genetics, and ecology of wolves are presented. Three issues for the conservation of wolves in southeast Alaska are discussed: loss of long-term carrying capacity for deer due primarily to extensive timber harvesting, increased mortality of wolves associated with improved human access from roads, and continued high levels of harvest of wolves by humans. Continued timber harvesting at current levels and by current methods will likely have adverse consequences for some segments of the wolf population. Although some short-term regulatory changes and the management of road access may need to be considered to keep wolf harvest at a sustainable level, the most important consideration is to maintain long-term carrying capacity for deer, the principal prey for most of the wolf population. A series of old-growth forest reserves may provide an effective strategy to increase the likelihood that wolves will persist where extensive timber harvesting has occurred, or is planned.

Keywords: Alexander Archipelago wolf, *Canis lupus ligoni*, effects of logging on wildlife, population dynamics of wolves, predator-prey dynamics, roads and wolf mortality, Tongass National Forest, southeast Alaska.

Summary

The Alexander Archipelago wolf (*Canis lupus ligoni*) occupies most of southeast Alaska from Yakutat Bay to Dixon Entrance except for Admiralty, Baranof, and Chichagof Islands. Based on common cranial characteristics, the Alexander Archipelago wolf was considered by early taxonomists to be a distinct subspecies. Recent taxonomic work suggests that these wolves may have originated from a larger subspecific group (*C. l. nubilus*) that at one time inhabited most of the contiguous Western United States. Wolves probably entered southeast Alaska sometime after the Wisconsin glaciation, following the northward expansion of black-tailed deer (*Odocoileus hemionus*) along the coast. The hypothesis of a southern origin is supported by recent genetic research showing that wolves in southeast Alaska share a common allele not found in a sample of wolves from interior Alaska or the Yukon. The population is relatively isolated from other wolf populations by water and mountain barriers.

A study of the ecology of wolves in southeast Alaska was conducted on Prince of Wales and Kosciusko Islands from 1992 to 1995. Average home-range size of radio-telemetered wolves was 280 square kilometers (109 mi^2), with 75 percent of the radio locations for each pack within “core areas” averaging 124 square kilometers (48 mi^2). Pack sizes ranged from 2 to 12, with 7 to 9 typical in early autumn. Annual rates of dispersal averaged 39 percent; 71 percent of dispersers were adults ≥2 years old. Dispersal distances were relatively short (13 to 182 kilometers [5 to 71 mi]) presumably due to inter-island water barriers. Wolf movements were more restricted during the denning and pup-rearing season (mid-April through August), when home ranges were 50 percent smaller than in winter. Of the 14 dens located in this study, all were in old-growth forest within 100 meters (328 feet) of fresh water. One den was under a large log; all others were in cavities beneath the roots of large trees.

Sitka black-tailed deer (*O. h. sitkensis*) were the primary prey of wolves. Deer remains occurred in 90 percent of wolf feces (scats) examined from Prince of Wales Island. Deer occurred exclusively in 45 percent of the scats. The only other prey occurring with >10 percent frequency was beaver (*Castor canadensis*). Other prey consumed in small quantities included black bears (*Ursus americanus*), mustelids, other small mammals, birds, and salmon (*Oncorhynchus* spp.). Using information on diet composition, consumption rates, and body size of prey, we estimated that wolves on islands in southern southeast Alaska consumed an average of 26 deer per wolf per year (SE = 4.1).

Most of the wolves in southeast Alaska occur on the large islands south of Frederick Sound. These islands (game management units 2 and 3) support approximately 60 to 70 percent of the total population. By extrapolating from empirical population estimates for Prince of Wales Island, we estimated the autumn 1994 population of wolves in southeast Alaska at slightly over 900 animals (SE = 216). Hunting, trapping, and illegal killing accounts for a high percentage of the mortality in wolves. Based on analysis of trapping and hunting mortality by wildlife analysis area (WAA), we determined that mortality was correlated with the linear kilometers of road within WAAs. Indeed, reported wolf harvest increased twofold when the length of road below 370 meters (1200 ft) elevation exceeded 95 kilometers (59 mi), regardless of the size of the WAA. This corresponded to an approximate road density of 0.4 kilometer per square kilometer (≈0.7 mi/mi^2), most of which were open to human access. Between 1993 and 1995, the average annual mortality in a total sample of 24 radio-collared wolves on Prince of Wales Island was 50 percent (SE = 13 percent). If applied to the overall wolf population on Prince of Wales Island, this rate of mortality would not be sustainable.

Wolf populations are closely tied to population levels of their ungulate prey. For southeast Alaska, we predicted the number of deer required per wolf to attain equilibrium between deer and wolves by using a Monte Carlo simulation of a model that calculated equilibrium ratios for wolves and their ungulate prey. We assumed a high average finite rate of increase for deer (1.3), a mean predation rate of 26 deer per wolf per year, and a human harvest of deer equal to 21 percent of the annual increment. Our results suggest that 170 to 180 deer per wolf are needed for a 95-percent probability of equilibrium, provided that mortality of deer due to predation is primarily additive. We cannot suggest a minimum deer population because we do not know what would constitute a minimum viable wolf population either demographically or genetically. Nevertheless, if we expect to sustain the current post-denning population of 250 to 300 wolves on Prince of Wales Island (along with subsistence and sport harvests of deer) with a high probability of attaining equilibria, then sufficient habitat is needed to support 42,500 to 54,000 deer.

Our review raises a number of issues concerning the long-term sustainability of wolves in southeast Alaska. Many more data are needed on wolf population structure, genetic structure, and predator-prey relations to fully address these issues and the overall question of viability. The Alexander Archipelago wolf exists in small numbers in a rapidly changing insular environment. Projected growth in human population, increasing road access, and the continuing loss and fragmentation of high-quality deer habitat will increase the risk of not maintaining a viable, well-distributed population of wolves in southeast Alaska. The area of most immediate concern is game management unit 2, including Prince of Wales and Kosciusko Islands.

Management actions that address risks to wolf populations include modifying hunting and trapping regulations as necessary, limiting construction of new roads and effectively closing some existing ones, and modifying timber harvest strategies to minimize fragmentation and loss of critical deer winter range. Habitat to support a minimum density of 5 deer per square kilometer (13 deer/mi^2), where deer are the primary prey for wolves, would provide for current levels of deer harvest by hunters, trappers, and wolves. In areas less productive for deer, maintaining current densities of deer is particularly important. Setting aside contiguous blocks of habitat within each biogeographic province that are large enough to encompass at least one wolf pack core home range (200 square kilometers [76 mi^2]) would markedly increase the likely persistence of wolves, especially if the reserves contain high-quality deer habitat sufficient to support an average density of deer equal to 7 deer per square kilometer (18 deer/mi^2). The objective of maintaining undisturbed blocks of habitat within each biogeographic province is to assure the persistence of several wolf packs that will serve as source populations capable of replacing wolves that periodically disappear from adjacent disturbed lands.

Purpose and Need

In 1990, wolves in southeast Alaska were identified by a USDA Forest Service-sponsored interagency committee as a species for which there may be concerns about viability or distribution as a result of extensive timber harvesting in the Tongass National Forest.[1] In December 1993, the Biodiversity Legal Foundation (Boulder, CO) and an independent biologist from Haines, AK, filed a petition with the U.S. Fish and Wildlife Service (FWS) requesting that wolves in southeast Alaska be listed as a threatened subspecies pursuant to the Endangered Species Act of 1973, as amended. The FWS ruled that listing was not warranted at this time, but added: “However, it is clear by our analysis that without significant changes to the existing Tongass Land Management Plan, the long-term viability of the Alexander Archipelago wolf is seriously imperiled.”[2] Following that notice, this assessment was prepared under the auspices of the memorandum of understanding among the Forest Service, Alaska Department of Fish and Game, and the Fish and Wildlife Service. They, along with the Regional Forester, Alaska Region, requested that a conservation assessment be prepared to summarize available scientific information on the status and ecology of wolves in southeast Alaska, and to identify issues regarding their long-term viability and distribution.

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[1] Suring, L.; Crocker-Bedford, D.C.; Flynn, R.W. [and others]. 1993. A proposed strategy for maintaining well-distributed, viable populations of wildlife associated with old-growth forests in southeast Alaska. Review draft. 278 p. On file with: U.S. Department of Agriculture, Forest Service, Alaska Region, P.O. Box 21628, Juneau, AK 99802-1628.

[2] U.S. Fish and Wildlife Service. 1994. Report on petition to list the Alexander Archipelago wolf under provision of the Endangered Species Act, 12 month finding; under signature of Mollie Beattie, Director. 25 p. (p. 19). On file with: Alaska Department of Fish and Game, Douglas, AK 99824.

This conservation assessment was chartered under the Tongass [National Forest] Land Management Plan revision and the interagency memorandum of understanding (MOU) among the Alaska Region of the Forest Service, the Alaska Region of the U.S. Fish and Wildlife Service, and the Alaska Department of Fish and Game to conserve species tending toward listing.[3] Our report summarizes the most current information available on the taxonomy, genetics, distribution, ecology, and population dynamics of wolves in southeast Alaska. Much of the information has not been published. In particular, we have drawn heavily from ongoing studies on wolves in southeast Alaska that is cosponsored by the USDA Forest Service, the Alaska Department of Fish and Game, the U.S. Fish and Wildlife Service, and the University of Alaska, Fairbanks. Results from that work are preliminary.

Contents

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[3] The primary objective of the MOU was to foster interagency cooperation for the conservation of candidate and sensitive species to avoid the need for listing and protection under the Endangered Species Act. The wolf, in addition to the marbled murrelet (*Branchyramphus mamoratus*) and northern goshawk (*Accipter gentilis*), was identified as a priority species for conducting a conservation assessment to achieve MOU objectives.

Background

A Brief Description of Southeast Alaska

Southeast Alaska comprises a narrow strip of mainland and a chain of islands known as the Alexander Archipelago wedged between the Pacific Ocean and the Coast Mountains of Canada (fig 1). The archipelago includes hundreds of islands ranging in size from less than 1 hectare (2.4 acres) to over 6,000 square kilometers (2,340 mi^2) that extend over 500 kilometers (310 mi) in a line parallel to the mainland. Elevations less than 800 meters (≈2,500 ft) are covered by temperate rain forests of Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), and Alaska-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach.) interspersed with muskegs. Subalpine and alpine zones of vegetation exist above 800 meters (≈2,600 ft), with the highest elevations covered by rock and ice. Several river drainages connect the region to interior British Columbia and the Yukon. Weather conditions are highly variable, with annual precipitation ranging between 130 and 400 centimeters (≈50 to 160 in). Accumulation of snow is greatest on the mainland and northernmost islands and becomes intermittent in the southern portion of the archipelago. About 80 percent of the land in southeast Alaska is contained within the Tongass National Forest, the largest National Forest in the United States.

Description and Distribution of Alexander Archipelago Wolves

Based on a sample of 37 wolves representing most of the Alexander Archipelago and the adjacent mainland, taxonomist E.A. Goldman described the Alexander Archipelago wolf (*Canis lupus ligoni*) as smaller, shorter haired, and darker in normal coloration than wolves in northern and interior areas of Alaska (Goldman 1944). Wood (1990) also described the Alexander Archipelago wolf as smaller with shorter and coarser hair than interior Canadian or Alaskan wolves. On islands in the southern portion of the archipelago, a black color phase constitutes about 20 percent of the population, gray or brown about 80 percent, and white or nearly white wolves less than 1 percent (Wood 1990). On the northern mainland, the black color phase is more common, accounting for about 50 percent of the wolves in the harvest (Morgan 1990). Adult wolves in southeast Alaska weigh an average of 39.5 kilograms (87 lb), with females weighing about 6.8 kilograms (15 lb) less than males (Alaska Department of Fish and Game [ADFG] 1960, Wood 1990). Wolves from some of the major island groups in the archipelago may be somewhat smaller than the average for the region. For example, adults from a sample of 24 radio-collared wolves from Kosciusko and Prince of Wales Islands averaged 34 kilograms (75 lb) (n =11, SE = 4.5 kilograms [10 lb]), with females weighing about 1 kilogram (2.2 lb) less than males (Person and Ingle 1995).

Wolves occur on the mainland and all larger islands in southeast Alaska except Admiralty, Baranof, and Chichagof Islands (fig. 2). Klein (1965) hypothesized that wolves colonized the region from the south following the postglacial northward expansion of black-tailed deer (*Odocoileus hemionus*). Carbon-14 dates of fossil bones from deer found on Prince of Wales Island suggest that deer arrived at least 8,000 years B.P. (Jull 1993). Although most of the islands in the southern half of the archipelago are used by wolves, only the largest, including Prince of Wales, Kuiu, Kupreanof, Mitkof, Etolin, Revillagigedo, Kosciusko, and Dall Islands, likely support packs of wolves that persist longer than a few years. For example, Prince of Wales and the islands immediately adjacent to it (including Kosciusko and Dall Islands)

Figure 1—Southeast Alaska and the Tongass National Forest (USDA Forest Service 1991).

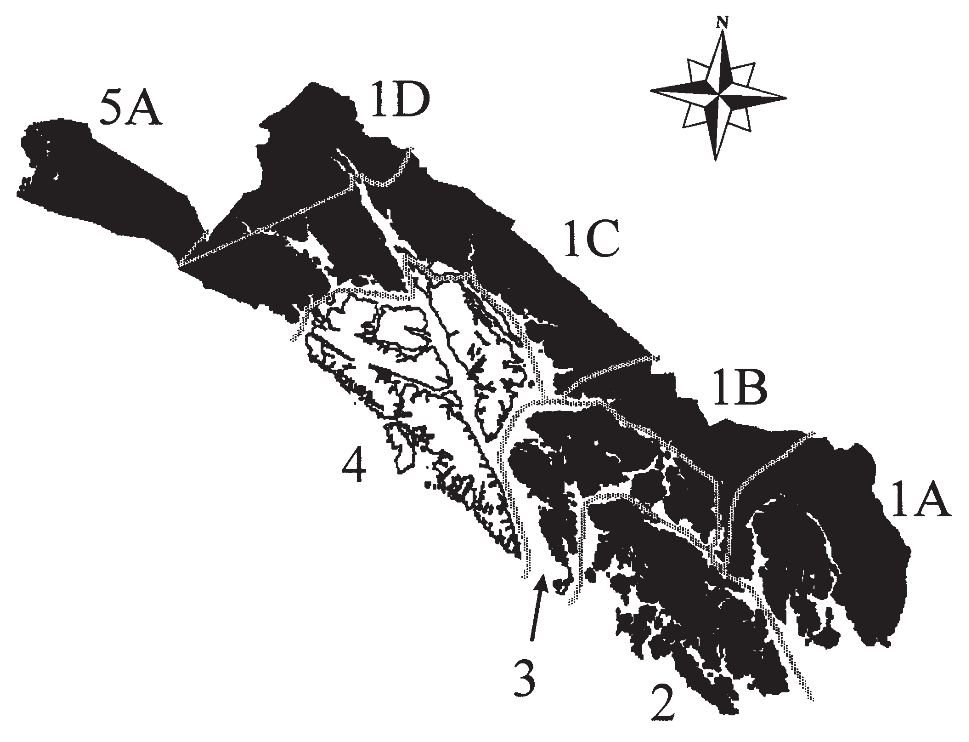

Figure 2—Distribution of Alexander Archipelago wolves in southeast Alaska. Wolves occupy areas shown in black. Map also shows game management units (GMUs) in southeast Alaska.

constitute game management unit 2 (GMU 2, fig. 2), so-designated by the ADFG. Within GMU 2, only the three largest islands—Prince of Wales, Kosciusko, and Dall—are known to have been continuously occupied by wolves for more than 20 years (Person and Ingle 1995). Wolf packs may include several smaller islands (e.g., Baker, Lulu, Noyes, Tuxekan, Marble, Thorne) in their home ranges or may exclusively inhabit smaller islands for a few years, but they are unable to persist permanently (Klein 1996, Person and Ingle 1995).

From a continental perspective, wolf populations in southeast Alaska are relatively isolated. The Coast Mountains to the east are glaciated or snow-covered year-round, and only six rivers or passes penetrate the 800 kilometers-long (500-mi) cordillera. The most significant of these are the Stikine, Taku, Whiting, and Unuk Rivers. Although no direct evidence exists regarding the dispersal of wolves through these passes or river valleys, wolves do occur in the valleys, and some level of interchange between interior Canada and the coast may occur. Nevertheless, the significant morphological differences between southeast Alaskan wolves and wolves from interior Canada and Alaska (Friis 1985, Nowak 1983, Pedersen 1982) suggest that the level of interchange is small or admixture has occurred only recently.

Within the Alexander Archipelago, dispersal of wolves among individual islands (or island groups) probably is restricted by water barriers. The absence of wolves (or wolf fossils) on the northern islands of the archipelago attests to the effectiveness of Frederick Sound, Stephen’s Passage, and Icy Strait as barriers to movement by wolves. Dense populations of brown bears (*Ursus arctos*) on Admiralty and Chichagof Islands also may contribute to the lack of successful colonization by wolves. Clarence Strait, which runs north-south along the eastern shore of Prince of Wales Island, restricts movement from the mainland and from Revillagigedo Island to GMU 2. Although wolves may reach Prince of Wales Island from the mainland via a chain of stepping-stone islands at the north end of Clarence Strait, at least eight directed swims (some 1.6 to 3.2 kilometers [1 to 2 mi] long) would be needed to complete such a crossing. Evidence exists suggesting that wolves are capable of swimming up to 4 kilometers (2.5 mi; Person and Ingle 1995), but the shapes and distribution of land masses, currents, and the high frequency of storms combine with distance to impede dispersal among the major island groups in the archipelago. Exchange between mainland and island populations is probably greatest in the vicinity of Mitkof Island and the Stikine River Delta, where the swimming distance is short at low tide. Water barriers between some major island groups and the mainland also could limit interchange between these island wolves and wolves immigrating from interior Alaska or Canada.

Wolves in southeast Alaska are legally hunted and trapped. A maximum of five wolves per hunter may be shot from 1 August to 30 April. Trappers may harvest wolves from 10 November to 30 April with no bag limit. The annual reported harvest in southeast Alaska from 1990 to 1995 has averaged about 194 wolves (SE = 35, GMUs 1 to 5). Hunting and trapping seasons are regulated and administered by the ADFG through the Board of Game. Subsistence hunting and trapping on Federal public lands are regulated and administered by the Federal Subsistence Board. State and Federal regulations regarding wolf harvest currently are identical.

Taxonomy

Early taxonomists recognized 24 subspecies of gray wolves (*Canis lupus*) in North America (Goldman 1944, Hall 1981) based on morphometric analyses of skull characteristics. Wolves from southeast Alaska were included in this classification as a subspecies, *C. l. ligoni*, unique to the Alexander Archipelago; their range extended from Dixon Entrance north to Yakutat Bay including the coastal mainland and all islands south of Frederick Sound. Pedersen (1982) performed an extensive morphometric analysis of wolves in Alaska by using a transect sampling strategy to determine if the four Alaskan subspecies (*C. l. pambasileus*, *C. l. tundrarum*, *C. l. alces*, and *C. l. ligoni*) described by Goldman constituted gradual clinal variations or distinct, geographically correlated populations. Pedersen (1982) reported that the three subspecies from interior Alaska (*C. l. pambasileus, C. l. tundrarum*, and *C. l. alces*) are indistinguishable from each other and probably represented clinal variation within a single population, but concluded that the abrupt morphometric differences between *C. l. ligoni* and interior Alaskan wolves suggest that wolves from southeast Alaska are a distinct population, possibly warranting subspecific classification. Nowak (1983) and Friis (1985) also concluded that *C. l. ligoni* is morphometrically distinct from interior Alaskan and Canadian wolves; nevertheless, both authors suggested that the Alexander Archipelago wolf is related to wolves that historically occupied coastal British Columbia, Vancouver Island, and the contiguous Western United States. Nowak (1996) recently proposed a revised taxonomy for extant populations of wolves in which *C. l. ligoni* is considered an isolated population of *C. l. nubilus* (fig. 3), a subspecies including wolves in central Canada and Minnesota. This latest taxonomic revision is likely to be the most widely accepted system among biologists and taxonomists. Regardless of the subspecific status of *C. l. ligoni*, morphological data strongly suggest a southern affinity, supporting the hypothesis that wolves colonized southeast Alaska from the south. As taxonomist Ronald Nowak (1994) pointed out in his letter:

> The original wolf populations of the entire western United States, and probably of coastal British Columbia, have been extinct for many years. Wolves of another subspecies have recently expanded into much of southwestern Canada and the northwestern United States. Essentially, the wolf population of Southeast Alaska is surrounded on one side by the sea and on the land side by wolves of another subspecies. It is probably isolated from its nearest living relatives (Minnesota to central Canada) by about 2,000 miles.
>
> The Southeast Alaska wolf population also can be viewed as a remnant U.S. population.…It is as distinctive a population segment as can be found among North American wolves.

Genetics

Studies incorporating allozyme electrophoresis of nuclear DNA (Kennedy et al. 1991) and restriction fragment analysis of mitochondrial DNA (mtDNA; Wayne et al. 1992) concluded that wolf populations in North America show little genetic differentiation among geographic regions. Wayne et al. (1992) identified 13 mtDNA genotypes in a sample of wolves representing most of their current range in North America and estimated sequence divergence to be small, ranging from 0.10 percent to 0.83 percent. Indeed, one genotype was virtually ubiquitous and occurred in wolves from Manitoba, northern Alaska, Yukon, Alberta, Montana, and Vancouver Island.

These data from mtDNA contrast with the current taxonomic system that recognizes 24 distinct subspecies of wolves in North America. At the very least, they support the revised taxonomic system proposed by Nowak (1996) that identifies only five distinct groups, and may suggest that wolves in North America are a single large population (Wayne et al. 1992). Nonetheless, genetic data are based primarily on results from restriction fragment analysis of mtDNA, which is informative only above the level of 0.5 percent genetic divergence (Shields 1995) and may have insufficient resolution to detect recent divergence in wolf populations. Further, none of the genetic studies included *C. l. ligoni* in the samples.

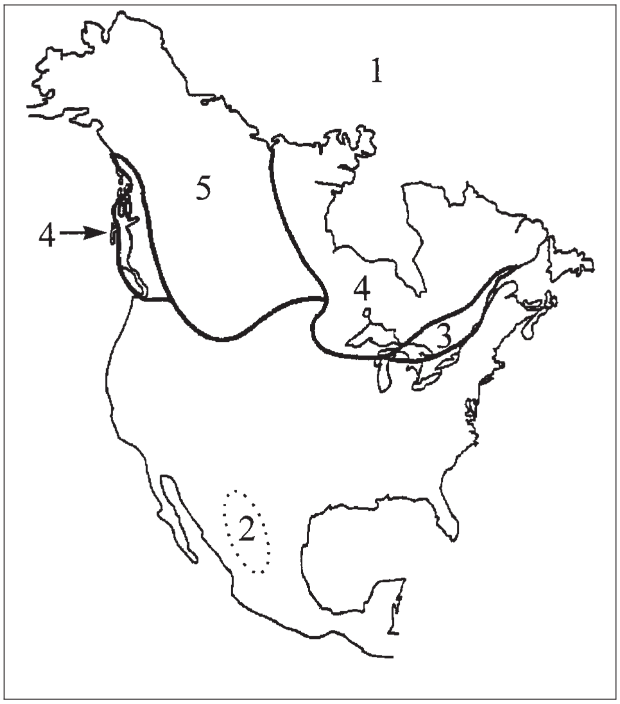

Figure 3—Current distribution of gray wolf subspecies in North America reflecting the revised taxonomy proposed by Nowak (1996): (1) *Canis lupus arctos*, (2) *C. l. baileyi*, (3) *C. l. lycaon*, (4) *C. l. nubilus*, and (5) *C. l. occidentalis*. Map is adapted from Nowak (1996) and range boundaries are approximate.

Results from a preliminary genetic analysis of mtDNA from *C. l. ligoni* identified a fixed allelic substitution in wolves from southeast Alaska distinct from those surveyed in northern Alaska and the Yukon (Shields 1995). In addition, genetic variation at eight other nucleotides within the mtDNA genomes of northern Alaska and Yukon wolves was not observed in any of the samples from southeast Alaskan wolves. This study used direct sequencing of a 310-base pair portion of the control region of PCR-amplified mtDNA, which is capable of detecting any genetic variation existing within the segment of the mtDNA genome surveyed. These data are significant because only a small portion of the mtDNA genome (<2 percent) was analyzed, thereby suggesting that additional genetic variation may exist within the entire genome. Nonetheless, sample sizes were small. Only 38 samples (29 from southeast Alaska, 9 from northern Alaska and the Yukon) from a total of 50 yielded amplified DNA adequate for analysis. A larger sample of wolves from outside southeast Alaska may reveal a closer affinity between *C. l. ligoni* and other Alaskan and Canadian wolves; nonetheless, data currently available suggest that the Alexander Archipelago wolf is distinct from wolves in northern Alaska and the Yukon (Shields 1995). The genetic relations between *C. l. ligoni* and wolves from coastal and interior British Columbia, Montana, and Minnesota have not been investigated. Shields (1995) speculates, based on the revised wolf taxonomy of Nowak (1996), that the Alexander Archipelago wolf may show genetic affinity with historic wolf populations from coastal British Columbia and Vancouver Island.

Shields (1995) observed no evidence that genetically unique subpopulations of wolves occur on individual islands within the Alexander Archipelago. One DNA cytotype occurred on six different islands, thereby suggesting that some gene flow exists across water barriers. Alternatively, 12 DNA cytotypes occurred among Alexander Archipelago wolves, indicating that genetic diversity was not being reduced by bottlenecking (Shields 1995). These data are limited because of small sample sizes, and no analysis of allelic frequency was possible. In addition, analyses of nuclear DNA, rather than mtDNA, may be necessary to resolve questions about gene flow and rates of migration within the Alexander Archipelago wolf population. Data suggest that migration events have occurred in the past, but are uninformative about the frequency of migration because mtDNA genotypes are transmitted intact through the female germ line and may proliferate in a population through a small number of matriarchal lines (Lehman et al. 1991).

Ecology

Home range and pack size—Wolves are social animals that travel in packs and actively defend territories from encroachment by other individuals or packs (Mech 1970). In southeast Alaska, minimum convex polygon (MCP) home ranges for wolf packs on Revillagigedo Island averaged 279 square kilometers (108 mi^2; range 79 to 447 square kilometers [30 to 170 mi^2], *n* = 7; Smith et al. 1987). On Prince of Wales and Kosciusko Islands, pack home ranges (average of 95-percent adaptive kernel [Worton 1989] and 95-percent MCP home ranges) based on a minimum of 40 independent radio locations averaged 280 square kilometers (109 mi^2; range 101 to 419 square kilometers [39 to 163 mi^2], *n* = 7; Person, in prep.). Core areas where wolf activity was concentrated, were estimated to be 124 square kilometers (48 mi^2) and were 55 to 60 percent smaller than total home ranges (based on the average of 75 percent adaptive kernel and 75 percent MCP home ranges).

MCP home ranges of packs (based on a minimum of 40 independent radio locations) during the denning and pup-rearing period (15 April-1 August) were about 50 percent smaller than during other times of the year (Person and Ingle 1995). This result contrasts with other studies that note wolf home ranges during summer and winter to be similar in size (Fritts and Mech 1981, Fuller 1989, Potvin 1988, Van Ballenberghe et al. 1975). Summer home ranges reported for wolves on Prince of Wales Island were not unusually small when compared with summer home ranges reported elsewhere for well-established wolf packs that primarily preyed on deer; however, winter home ranges were substantially larger than those reported in other studies. For example, Fuller (1989) reports average winter and summer home ranges of 116 and 110 square kilometers (45 and 43 mi^2), respectively, for wolves in a portion of Minnesota where deer density was high. On Prince of Wales Island, summer home ranges for five wolf packs averaged about 100 square kilometers (39 mi^2) whereas winter home ranges for the same packs averaged about 240 square kilometers (93 mi^2; Person, in prep.).

Pack sizes on Revillagigedo Island averaged 5.4 wolves (range 2 to 12, *n* = 8; Smith et al. 1987). Pack sizes on Prince of Wales and Kosciusko Islands were larger, averaging 7 to 9 wolves (range = 2 to 12, *n* = 8; Person and Ingle 1995) in early autumn before the trapping season. Pack size and composition can change over time, with individuals or small groups of wolves occasionally splitting from the main pack, only to rejoin it days or weeks later (Person, in prep.). Indeed, all members of a wolf pack rarely are observed together, except during winter. Pack sizes are difficult to estimate unless repeated, direct observations are made.

Food habits—Wolves prey on large ungulates such as deer, mountain goats (*Oreamnos americanus*), moose (*Alces alces*), caribou (*Rangifer tarandus*), and elk (*Cervus elaphus*) (Mech 1970). In southeast Alaska, deer are the primary prey on the islands and portions of the mainland (Garceau 1960, Kohira 1995, Smith et al. 1987). In areas of the mainland where deer are scarce, important prey include beaver (*Castor canadensis*), mountain goat, and moose (Smith et al. 1986a, Wood 1990). Wolves in southeast Alaska have access to spawning salmon during late summer and early autumn (Kohira 1995, Smith et al. 1986b, Wood 1990). Wolves also feed opportunistically on harbor seals (*Phoca vitulina*), mustelids, small mammals, birds, and marine invertebrates (Garceau 1960; Kohira 1995; Merriam 1966, 1968; Smith et al. 1986b).

Data from 182 microscopically examined wolf scats collected between autumn 1992 and autumn 1994 on Prince of Wales Island showed deer remains in 90 percent of the scats (Kohira 1995). Deer occurred exclusively in 45 percent of the scats, but often were found in conjunction with beaver (30 percent of the scats). The remains of beaver, the only other prey species that occurred with >10 percent frequency, were found in 31 percent of the scats, with the highest incidence occurring during late spring. Only one scat contained exclusively beaver remains. Other prey consumed in small quantities included black bear (*Ursus americanus*), mink (*Mustela vison*), marten (*Martes americana*), river otter (*Lutra canadensis*), small mammals, birds, and fish (Kohira 1995).

In a sample of 363 scats from Revillagigedo Island, 74 percent and 20 percent of the scats contained deer and beaver remains, respectively (Smith et al. 1987). About 30 percent of the scats collected in summer contained remains of fawns, accounting for 41 percent of all scats containing deer.

We combined the data from Prince of Wales and Revillagigedo Islands (n = 545 scats) and estimated the percentage of prey species by volume in the diet by using a regression model described by Floyd et al. (1978) and later modified by Weaver (1993). Results of a Monte Carlo simulation (n = 1,000) of the regression function indicated that 77 percent (SE = 10 percent) of the diet was composed of deer. Beaver composed only 13.7 percent (SE = 9 percent) of the diet, and all other species contributed <10 percent. These data strongly suggest that wolves occurring on the islands of southeast Alaska depend on the availability of deer and raise questions about the ability of alternative prey to sustain wolves in the absence of deer.

Population dynamics—

Reproduction and denning—Age of first breeding is about 22 to 34 months, and litters of 3 to 7 young usually are produced (Mech 1970, Stephenson 1989). Most packs include a pair of breeding adults plus adults that may or may not breed. Mean litter sizes in Alaska, as indicated by counts of blastocysts, range from 4.6 to 7.2, depending on prey availability per wolf (Boertje and Stephenson 1992, Gasaway et al. 1992). The reproductive potential of wolves is high, and natural or human-caused mortality, rather than the failure of a pack to breed or produce pups, often is the major factor limiting the growth of wolf populations (Fuller 1989, Rausch 1967).

Wolves in southeast Alaska use dens, or areas near dens, from mid-April through early July. Activity peaks around den sites from early May to the third week in June. Of 14 den sites examined between October 1992 and October 1995, all were in old-growth forest within 100 meters (330 ft) of fresh water (Person and Ingle 1995). One den was under a large log; all others were in cavities beneath the roots of large trees (mean diameter at breast height >90 centimeters [35 in]). Eight of 11 dens visited during the year they were used were adjacent to ponds or streams with active beaver colonies.

Litter sizes estimated from direct observations at dens on Prince of Wales Island ranged from one to six pups ($\bar{x}$ = 3.7, SE = 1.8, n = 6) during the 1995 denning period (Person, in prep.). Direct observations made during early autumn revealed that only one pup from the total number seen at the dens had disappeared, suggesting high pup survivorship during summer. This outcome may be a consequence of the availability of salmon at the time pups are weaned, enabling them to exploit an additional food supply at a time when they are inexperienced hunters and occupy a low position in the dominance hierarchy of the pack.

Mortality—Humans account for a high percentage of mortality in both protected and heavily exploited wolf populations (Ballard et al. 1987, Fuller 1989, Peterson et al. 1984). In southeast Alaska, 1,163 wolves were reported killed by hunters and trappers from 1990 to 1995. About 60 percent of the mortality was from trapping (including snaring) and 40 percent from hunting (i.e., ground shooting).[1] The highest reported mortality occurred in December and January during the peak of the trapping season.

In exploited populations, mortality from natural causes (e.g., starvation, accidents, disease, and fighting) is small, typically averaging 5 to 10 percent per year (Fuller 1989). A more substantial cause of mortality results from unreported or illegal killing of wolves by people. Of 17 radio-collared wolves on Prince of Wales Island that died during a 3-year study, nine (53 percent) were legally killed by humans, five (29 percent) were killed by humans, but not reported, and three (18 percent) died from natural causes (Person, in prep.). Considering the additive effects of natural and unreported mortality, total mortality could be 35 to 50 percent higher than that reported. Some bias may exist against reporting legally killed wolves with radio collars; therefore, the actual unreported mortality from hunting or trapping may be less than that suffered by radio-collared wolves. Nevertheless, reported mortality may substantially underestimate total mortality.

The highest annual harvest of wolves in southeast Alaska is in GMU 2. To estimate mortality we pooled sex and age classes and used a staggered-entry Kaplan Meir survival rate estimation method (Pollock et al. 1989) with 2-week intervals. Total mortality (natural, legal, and illegal harvest) in a sample of 19 radio-collared wolves from autumn 1993 to spring 1994 was 61 percent (SE = 11 percent); mortality in a sample of 13 radio-collared wolves from autumn 1994 to spring 1995 was 38 percent (SE = 13 percent) (Person and Ingle 1995; Person, in prep.). Lower mortality in the second year reflected a shift in trapping effort to the southern half of GMU 2, away from the study area. From these estimates, the most probable average annual mortality in the study area on Prince of Wales and Kosciusko Islands for June 1993 to June 1995 was 50 percent (SE = 13 percent, total sample for both years was 24 individual wolves).

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[1] Alaska Department of Fish and Game. Unpublished data. On file with: Division of Wildlife Conservation, Douglas, AK 99824.

Fuller (1989) suggests that a 35-percent rate of total mortality for wolves could result in declines. Other studies have reported populations declining when multiyear mortality ranged between 25 and 40 percent (Gasaway et al. 1983, Keith 1983, Peterson et al. 1984). Wolves occupying islands (or other insular areas) in southeast Alaska will likely be more vulnerable to overexploitation simply because mortality cannot be readily compensated for by immigration from adjoining areas.

Dispersal—Pups that survive to adulthood either remain in their natal pack or disperse. Dispersers may form associations with other wolves, occupying vacant areas adjacent to established territories of packs (Ballard et al. 1987, Fritts and Mech 1981, Gese and Mech 1991, Peterson et al. 1984). In wolf populations where mortality is high, lone wolves may be more successful in finding vacant territories in which to settle or in being accepted into other established packs (Ballard et al. 1987, Fritts and Mech 1981). Successful dispersal is most often short in duration (Fritts and Mech 1981, Gese and Mech 1991, Peterson et al. 1984). Dispersing wolves are more vulnerable than nondispersers to hunting and trapping and are more likely to be killed by other wolves (Peterson et al. 1984). Dispersing radio-collared wolves on Prince of Wales Island suffered 71 percent (SE = 17 percent) mortality between June 1993 and June 1994, and 67 percent mortality (SE = 19 percent) between June 1994 and June 1995, compared with 50 percent (SE = 15 percent) and 14 percent (SE = 13 percent) for resident wolves during these same periods (Person, in prep.). This mortality level is consistent with that reported by Peterson, et al. (1984) for the Kenai Peninsula in Alaska where dispersing wolves suffered 37 percent higher mortality than resident wolves.

Wolves usually disperse singly and may make several temporary forays from the main pack before leaving permanently (Fritts and Mech 1981, Fuller 1989, Van Ballenberghe 1983). The average age of dispersing wolves in south-central Alaska was 30 to 33 months, with 40 percent of dispersing females and 50 percent of dispersing males under 24 months of age (Ballard et al. 1987). During one study in Minnesota, 17 percent of the adults, 49 percent of the yearlings, and 10 percent of the pups dispersed from packs each year (Fuller 1989). In the largest study of wolf movements to date, Gese and Mech (1991) report that 75 wolves (24 percent) dispersed out of 316 wolves monitored over 21 years in Minnesota. During their study, 8 percent of adults, 75 percent of yearlings, and 16 percent of pups dispersed (Gese and Mech 1991). On Prince of Wales Island, the annual rate of dispersal was 39 percent, with adults (≥2 years old) composing 71 percent of all dispersers (Person and Ingle 1995). The high rate of dispersal by adults may be a response to human exploitation. Sexually mature wolves may be induced to disperse from natal packs because of the availability of nearby vacant territories created by hunting or trapping pressure. They may be better able to hold on to these new territories than younger wolves because of age and experience (Gese and Mech 1991). In the case of the Kosciusko Island pack, two of three radio-collared wolves (one adult, one yearling) dispersed long distances (>160 kilometers [100 mi]; Person and Ingle 1995), possibly because of low prey availability. Dispersal induced by low prey availability has been observed in several wolf studies (Fritts and Mech 1981, Gese and Mech 1991, Peterson et al. 1984).

Dispersal may be restricted between major island groups and the mainland; however, dispersal among islands in close proximity (<1 kilometer [0.6 mi] apart) may be common. For example, two wolves captured and radio collared on Kosciusko Island dispersed in 1994; one was subsequently located on the southern tip of Dall Island, and the other eventually was found near the southern tip of Prince of Wales. The wolf located on Dall Island traveled a minimum distance of 182 kilometers (113 mi) involving at least two swims >350 meters (1,145 ft) (Person and Ingle 1995). The other wolf moved at least 160 kilometers (100 mi) from its origin. None of the 13 radio-collared wolves on Prince of Wales or Kosciusko Islands that eventually dispersed swam across Clarence Strait, or to other islands >1 kilometer (0.6 mi) from Prince of Wales Island.

Population size and trends—Estimates of wolf population size published in annual survey and inventory reports (e.g., Morgan 1990) are based on anecdotal observations made by trappers, hunters, and ADFG biologists. No estimate of accuracy or precision can be attached to these figures. Alternatively, population size can be estimated if the number of packs, pack size, and home ranges of packs are known. By using such data from packs containing radio-collared wolves (Person and Ingle 1995) in a simulation model (appendix 1), the wolf population on Prince of Wales and Kosciusko Islands was estimated to be 321 wolves (SE = 135) during autumn 1994 and 199 wolves (SE = 111) during spring 1995. The smaller population in spring reflected overwinter mortality, primarily from trapping. Eighty-five wolves were reported killed in GMU 2 during the 1994-95 hunting and trapping seasons.[2] This level is almost certainly an underestimate of total mortality, however.

These estimates for Prince of Wales and Kosciusko Islands can be refined by comparing them to observed densities of wolves. In autumn 1994, 41 resident wolves were observed within an 1,800-square kilometer (700-mi^2) area of Prince of Wales and Kosciusko Islands. This corresponded to a density of 22.7 resident (nondispersing) wolves per 1,000 square kilometers (6 wolves per 100 mi^2) and a population estimate for Prince of Wales and Kosciusko Islands of 154 resident wolves. At any point in time, about 29 percent (SE = 9 percent) of the wolf population consists of dispersers (Person, in prep.); therefore, the total population estimate would be 217 (SE = 65) wolves.[3] Simulations overestimated these empirical results by 32 percent.

The difference is likely the result of not all land area being occupied by wolves, which results in an overestimate in the simulated population. The population of wolves used to derive the empirical estimate of density also was intensively trapped for 3 years and therefore may underestimate density for wolves exposed to lower mortality from trapping. The average of the two estimates is 269 (SE = 80) wolves and likely represents the best estimate for Prince of Wales and Kosciusko Islands. The same procedure applied to the population estimate in spring 1995 yielded a population of 174 (SE = 68) wolves. These estimates suggest that overwinter mortality in 1994-95 on Prince of Wales and Kosciusko Islands was 35 percent, which was consistent with the 38-percent mortality estimated from survival of radio-collared wolves during that same period.

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[2] Alaska Department of Fish and Game. Unpublished data. On file with: Division of Wildlife Conservation, Douglas, AK 99824.

[3] Total population estimate = resident wolves/percent residents in population = 154/(1-0.29) = 217.

Our fall population estimate represents a density of 39 wolves per 1,000 square kilometers (390 mi^2), which is consistent with densities of wolves reported in other areas where deer are the primary prey (table 1). Prince of Wales and Kosciusko Islands represent 80 percent of the total land area in GMU 2. Expanding the population estimate proportionately, the estimated number of wolves in GMU 2 in autumn 1994 was 336, and in spring 1995 was 217. Because data for pack-size and home-range are not available from other areas of southeast Alaska, estimates of total population size can be made only by making assumptions about the contribution of GMU 2 in comparison with other GMUs. Based on results from a model linking wolf numbers to habitat capability for deer and other prey, GMU 2 probably represents about 37 percent of the total wolf population in southeast Alaska (Suring and Degayner 1988) (fig. 4). From this, we estimated the fall 1994 population of wolves in southeast Alaska, before the trapping season, to be about 908 (SE = 216). The large standard error of this estimate is certainly an underestimate of the true value, because the model used to estimate the number of wolves from habitat capability for deer provided no estimate of variance.

Although mortality in our study area on Prince of Wales Island averaged 50 percent from June 1993 to June 1995, the actual population trend also is a function of reproduction. A simple Lotka-Leslie model (Noon and Biles 1990) can be used to estimate the finite rate of increase of the wolf population given survival and birth rates observed:

$$1 = \sum_{x=0}^{\infty} \frac{l_x b_x}{\lambda^x} \qquad (1)$$

where

l_x = survivorship to age class x,

b_x = number of female offspring per female of age x, and

λ = finite rate of increase assuming a stable-age distribution.

Survivorship is a function of survival rates such that $l_x = (s_{x-1})(s_{x-2})(s_{x-3})\ldots$,

where

s_x = annual survival rate for age class x.

Sample sizes were too small to estimate age-specific reproductive and survival rates; nevertheless, λ may be estimated if age classes are combined and it is assumed that wolves <2 years old do not breed (Mech 1970). The function can then be rewritten to solve for λ:

$$\lambda = \frac{s + (s^2 + 4s^2 b)^{1/2}}{2} \qquad (2)$$

where

s = survival rate, assuming survival for all age classes is equal, and

b = birth rate, assuming birth rates for all age classes are equal (assumes $b_0 = b_1 = 0$).

Table 1—Number of wolves per 1000 square kilometers (390 mi^2) reported during fall and winter in various areas of North America where deer are the primary prey

Location	Years	Wolves	Source
		Number	
Northeast Minnesota	1970-71	42	Van Ballenberghe et al. 1975
Northeast Minnesota	1967-69	40	Nelson and Mech 1986a
North-central Minnesota	1980-86	39	Fuller 1989
East-central Ontario	1969	36	Pimlott et al. 1969
Central Ontario	1958-65	38	Pimlott et al. 1969
Southern Quebec	1980-84	28	Potvin 1988
Vancouver Island	1983	44	Hatter and Janz 1994
Vancouver Island	1976	70	Hebert et al. 1982
Prince of Wales Island	1994	39	Person, in prep.

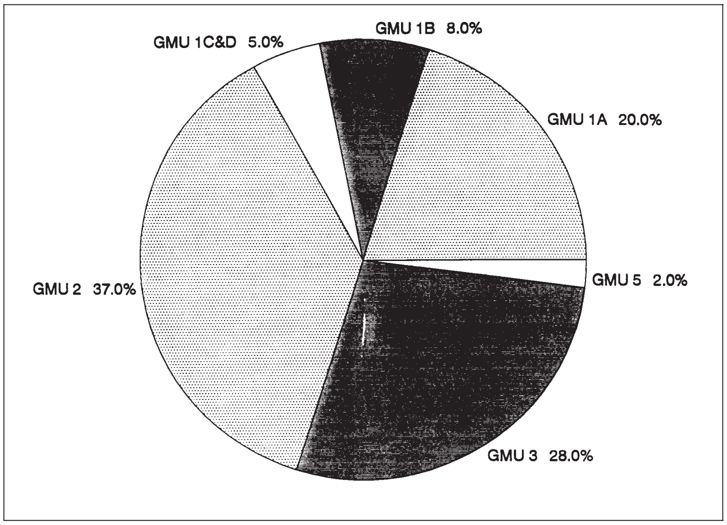

Figure 4—Distribution of wolf numbers in southeast Alaska by game management units (GMUs) as predicted by habitat capability for deer (USDA Forest Service 1991).

The variance of this model can be approximated by the following equation:

$$\mathrm{Var}(\lambda) = \mathrm{Var}(s)\left(\frac{1+2b+\sqrt{4b+1}}{2}\right)^2 + \mathrm{Var}(b)\left(\frac{S^2}{4b+1}\right)^2 , \qquad (3)$$

assuming that s and b are not significantly correlated and are density independent (see appendix 2 for the derivation of these models). The model also represents a point estimate in time and assumes the wolf population is closed (a reasonable assumption for Prince of Wales and Kosciusko Islands). Survival rate is the most important factor influencing λ, with birth rates of secondary importance. Substituting 0.5 (SE = 0.13) for s and 0.52 (SE = 0.50) for b (see appendix 2 for how these values were estimated), we estimated λ to be 0.69 (SE = 0.23). Comparing this estimate with a simulated population with $\lambda = 1$ and SE = 0.23, the results are different ($t = 16.3$, $df = 14$, $P < 0.001$), thereby indicating that the population declined between June 1993 and June 1995. We caution that because of the limitations of the data, λ should be interpreted only with respect to the significance of the difference from one and not as a precise estimate of the actual value. These results are consistent with observations made in the field by biologists and trappers who believe that wolves on Prince of Wales and Kosciusko Islands were at a population peak during winter 1992-93 and have declined since, owing primarily to trapping and hunting (in GMU 2, 86, 105, 103, 85, and 99 wolves were reported killed during the 1991-92, 1992-93, 1993-94, 1994-95, and 1995-96 trapping seasons, respectively[4]). We cannot extrapolate from these results to assess population trends for wolves outside of GMU 2. Trapping records indicate that harvest intensity is probably greatest in GMU 2, but wolf numbers could be increasing or remaining stationary in other areas while declining in GMU 2.

Wolf-deer interactions**—**Much emphasis has been placed on the role of wolf predation in limiting or regulating ungulate populations (Gasaway et al. 1983, 1992; Mech 1970; Messier 1994; Peterson and Page 1988; Theberge 1990; Van Ballenberghe and Ballard 1994). The focus has been primarily on the effects of predation on moose and caribou. Most authors have concluded that wolf predation can limit moose and caribou populations under some circumstances, particularly when multiple predators, multiple prey species, or severe weather are involved (Gasaway et al. 1992, Van Ballenberghe and Ballard 1994).

Much less attention has been directed toward the quantitative analysis of predator-prey dynamics with respect to wolves and deer (Fuller 1989, Hatter and Janz 1994, Lewis and Murray 1993), although much is known qualitatively about the effects of wolf predation on deer (Fuller 1991; Hoskinson and Mech 1976; Nelson and Mech 1981, 1986b). In Minnesota, severe winter weather caused a decline in numbers of white-tailed deer (*Odocoileus virginianus*) in some areas (Mech and Karns 1977). Wolves delayed the recovery of these deer populations, but they did not cause the original decline (Mech and Karns 1977). Van Ballenberghe and Hanley (1984) hypothesized that three things tend to increase the probability of wolves suppressing deer populations in southeast Alaska: (1) periodic winters of deep snow that result in increased killing, (2) the patchiness of winter habitat for deer that reduces the time

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[4] Alaska Department of Fish and Game. Unpublished data. On file with: Division of Wildlife Conservation, Douglas, AK 99824.

wolves spend searching for prey, and (3) the availability of marine food resources that buffer wolves from cyclic fluctuations in their terrestrial prey. Mech and Karns (1977) report that in a declining deer herd, surviving deer inhabit overlapping edges of wolf-pack territories and wolves tend not to hunt in these areas, or buffer zones, to avoid potentially fatal encounters with their neighbors. Klein (1981) suggests that in southeast Alaska, where the boundaries of many pack home ranges are shorelines, the potential for wolves to reduce deer numbers is increased because there are fewer buffer zones among territories.

In the early 1960s, four wolves were transplanted to Coronation Island in an experiment to observe the effects of wolf predation on Sitka black-tailed deer (Klein 1996). The wolves reached a peak population of 13 after 4 years and apparently reduced deer numbers dramatically. As their food supply dwindled, the wolves declined in number. The last wolf on Coronation Island was shot in the late 1960s, ending the experiment (Merriam et al. 1994), and the deer population has since rebounded. Coronation Island is too small (78 square kilometers [30 mi^2]) and supports insufficient alternative prey to sustain wolves in the absence of deer. The experiment suggests that islands in southeast Alaska comparable in size to Coronation Island are unlikely to support wolves permanently unless they are near other land masses, thus enabling wolves to periodically emigrate or immigrate. Further, deer density probably was near carrying capacity when wolves were introduced (Klein 1996). Consequently, the resiliency of the deer population to wolf predation (i.e., its ability to offset mortality from predation by increasing reproduction) probably was limited because of lower reproductive rates in deer resulting from the overbrowsed and degraded condition of the habitat (Klein 1996). The results from Coronation Island suggest that if wolves and deer are confined to small islands of habitat, then predator-prey disequilibria may result.

The stability of deer and wolf populations depends on several factors, including the rate of predation by wolves, the number of deer killed by hunters and other predators, and the ratio of deer to wolves. The most important determinants, however, are the rate of growth of the deer population and the frequency of stochastic events such as severe winters. These latter factors are related to habitat quantity and quality. For example, as deer or other ungulate populations approach carrying capacity, intraspecific competition for food will reduce successful reproduction and increase chronic mortality (Caughley and Sinclair 1994; McCullough 1979, 1987) and thus reduce the fraction of the deer population that can be exploited by wolves and other predators without causing the prey population to decline. A predator-prey equilibrium (McCullough 1979) may result, in which predation reduces deer density sufficiently to stimulate greater reproduction in deer, thereby making more deer available to the predators. The stability of such an equilibrium is contingent on the availability of suitable habitat for deer, such that the deer population can maintain a rate of growth sufficient to offset losses to predation. Stochastic events, such as severe winters or reductions in the abundance and quality of suitable habitat, may perturb the conditions of equilibria and result in widely fluctuating wolf and deer populations. By limiting immigration and emigration of both deer and wolves, the insular conditions commonly encountered in southeast Alaska increase the probability that population fluctuations may end in local crashes of deer populations. The fluctuations exhibited by the population trajectories of wolves and moose on Isle Royale, MI, certainly illustrate the consequences of insularity with respect to a mammalian predator-prey community (Peterson and Page 1988).

The recovery of deer populations depends on the reproductive potential of the survivors, immigration from other areas, and the numerical response of wolves and other predators (including humans) to declining deer density. If alternative species of prey exist so that wolf numbers do not decline sufficiently to permit deer to increase (or if mortality of deer from hunting or other predators remains high), or if the reproductive potential of the deer population is reduced because of habitat loss, then recovery of deer populations after a crash could take a long time (Van Ballenberghe and Hanley 1984). For example, deer populations in GMU 3 (including Kuiu, Kupreanof, and Mitkof Islands) crashed during the early 1970s as a result of a series of hard winters (Olson 1979). In 1975, deer hunting in GMU 3 was halted completely and remained closed throughout most of the GMU for 18 years. Today, deer are still at levels far below carrying capacity over most of the GMU (Kirchhoff 1994). The persistently low deer numbers illustrate that interactions of deer and their predators (in this instance, wolves and black bears) may, under some circumstances, retard recovery of the deer population. Although deer also declined in GMU 2 following the same hard winters, snowfall on the more southern islands was not as heavy, and more of the landscape in GMU 2 was sheltered by productive old-growth forest. In marked contrast to the result in GMU 3, deer in GMU 2 did not decline as far and rebounded much more quickly after the hard winters.

The rate at which wolves kill large mammals ranges widely given the availability, size, and vulnerability of prey. Direct estimates of predation rates on Sitka black-tailed deer are not available. We therefore estimated predation rate by deriving a series of equations incorporating average weights of deer, proportion consumed by wolves, average weights of wolves, and their daily requirements for food intake. We calculated the weight of edible meat from each deer carcass:

$$w_{cons} = (w_{ad})(\phi_{ad})(\psi_{ad}) + (w_f)(\phi_f)(\psi_f)\,, \qquad (4)$$

where

w_{cons} = weight in kilograms of meat consumed per deer carcass,

w_{ad} = average weight in kilograms of adult deer,

ϕ_{ad} = proportion of adult deer carcass consumed,

ψ_{ad} = proportion of adults in the deer population,

w_f = average weight in kilograms of fawns,

ϕ_f = proportion of fawn carcass consumed, and

ψ_f = proportion of fawns in the deer population.

Next we estimated the weight of deer meat consumed per wolf per year:

$$C_{wolf} = (w_{wolf})(d_{wolf})(\Phi_{wolf})(365)\,, \qquad (5)$$

where

C_{wolf} = weight of deer meat in kilograms consumed per wolf per year,

w_{wolf} = average weight in kilograms of wolves,

d_{wolf} = daily per capita food requirement in kilograms of food per kilogram of wolf, and

Φ_{wolf} = proportion of deer in the diet.

Finally, an estimate of the number of deer killed per wolf per year (P_R) was calculated:

$$P_R = \frac{C_{wolf}}{w_{cons}}\,, \qquad (6)$$

and its variance:

$$\mathrm{Var}(P_R = \mathrm{Var}(w_{cons})\left(-\frac{C_{wolf}}{w_{cons}{}^2}\right)^2 + \mathrm{Var}(C_{wolf})\left(\frac{1}{w_{cons}}\right)^2\,, \qquad (7)$$

(for the parameter estimates used, see appendix 3). From inputting of parameter values appropriate for wolves and Sitka black-tailed deer in southeast Alaska, we estimated predation rate to be 26 deer per wolf per year (SE = 4.1). This calculation assumed that wolves exhibit a type I functional response (Holling 1966) resulting in the rate of predation remaining constant despite changes in the density of prey.

To evaluate the potential for equilibria between wolves and deer given our estimate of predation rate, we used a model proposed by Keith (1983) that combines predation rate, rate of growth of the prey population, and the fraction of the recruitment to the prey population removed by hunting or other predators to calculate the number of ungulate prey per wolf (equilibrium ratio) necessary for equilibrium to occur:

$$N = \frac{P_R}{(\lambda - 1)(1 - H)}, \text{ for } \lambda > 1 \text{ and } H < 1 \qquad (8)$$

where

N = number of deer per wolf necessary for equilibrium prior to parturition,

P_R = number of deer killed per wolf per year,

λ = finite rate of increase of deer in the absence of predation measured prior to parturition, and

H = fraction of annual recruitment to the deer population removed by hunting or other predators.

Van Ballenberghe and Hanley (1984) used this model, or equilibrium function, to explore the influence of changes in λ on equilibrium ratios brought about by habitat changes. They concluded that reductions in λ dramatically increase the number of deer per wolf needed for equilibrium and reduces the probability that stability between deer and wolves will occur. Unfortunately, the equilibrium function (eq. 8) is deterministic and does not reflect the uncertainty associated with the input parameters. We altered the model to correct for this attribute by replacing the input variables with random samples drawn from the probability density function (pdf) of each parameter as defined by their sampling distributions or some appropriate hypothetical distribution:

$$N' = \frac{P'_{R(a,b)}}{\left(\lambda'_{(a,b)} - 1\right)\left(1 - H'_{(a,b)}\right)}, \tag{9}$$

where

N' = vector of equilibrium solutions for the number of deer per wolf necessary for equilibrium prior to parturition,

$P'_{R(a,b)}$ = vector of random samples from the pdf of P_R with $\mu = a$ and $\sigma = b$,

$\lambda'_{(a,b)}$ = vector of random samples from the pdf of λ with $\mu = a$ and $\sigma = b$, and

$H'_{(a,b)}$ = vector of random samples from the pdf of H with $\mu = a$ and $\sigma = b$.

The model assumes that predation by wolves and other predators is a source of additive mortality, that λ encompasses all reproduction, immigration, emigration, and compensatory mortality, and that each input parameter is an independent random variable. The variance of N' may be approximated by the following equation:

$$\begin{aligned}\mathrm{Var}(N') = {} & \mathrm{Var}\left(P'_R\right)\left[\frac{1}{(\lambda-1)(1-H)}\right]^2 + \mathrm{Var}(\lambda')\left[-\frac{P_R}{(\lambda-1)^2(1-H)}\right]^2 \\ & + \mathrm{Var}(H')\left[\frac{P_R}{(\lambda-1)(1-H)^2}\right]^2\end{aligned} \tag{10}$$

A Monte Carlo simulation was conducted to estimate the equilibrium ratio for deer and wolves in GMU 2 using the following parameter estimates:

λ'—Connolly’s (1981) review suggests finite rates of increase as high as 1.4 for established populations of mule and black-tailed deer. For these model simulations, we assumed a relatively high λ ($\mu = 1.3$, SE = 0.05) because deer seem to be well below carrying capacity in GMU 2, based on browse and pellet group surveys (Kirchhoff 1993). About 95 percent of the values fell between 1.2 and 1.4.

P'_R—The analysis in this report suggests a predation rate of 26 deer per wolf per year in areas where deer are the primary prey species (>75 percent of the diet). Actual rates of killing attained will be higher or lower in any given year depending on availability of alternate prey, fawn-to-adult ratios in the kill, and snow conditions that make deer more or less vulnerable to wolves. Our estimate is higher than predation rates reported for wolf predation on white-tailed deer (Fuller 1989) because Sitka black-tailed deer are about 25 to 30 percent smaller. For these model simulations, we estimated the standard error for predation rate to be 4.1. Thus, 95 percent of the values fell between 18 and 34 deer per wolf per year.

H'—We assumed that the only other significant predation on deer in GMU 2 was from hunting. Although black bears do prey on fawns, the extent of this predation is unknown and no estimate is possible. Consequently, equilibrium ratios predicted by the simulation may underestimate the true values if bear predation is significant. In our simulation, the value *H* refers to the proportion of the annual increment (population increase) of deer removed each year by hunting. To obtain this value, we estimated the current deer population on Prince of Wales Island from surveys of deer pellet groups on winter range (productive old-growth forest below 450 meters [≈1,500 ft]) (Kirchhoff 1993, Kirchhoff and Pitcher 1988). From a standard conversion factor (Kirchhoff 1990), mean pellet-group density was converted to an equivalent deer density of 14.6 deer per square kilometer (38/mi^2; n = 11 watersheds). Assuming deer winter range is approximately equal to productive forest land, the current population of deer on Prince of Wales Island may be close to 42,000 deer (14.6 deer per square kilometer × 2895 square kilometer of winter range). Because this population estimate is lower than the habitat capability of 55,000 deer based on the USDA Forest Service (1996) model, we assumed a high finite rate of increase in the population (1.3). With the population growing at this rate, the annual increment is 12,600 deer (0.3 × 42,000). The average deer harvest from 1993 to 1995 on Prince of Wales Island was about 2,700 deer, which represented 21 percent of the annual increment.[5] In the model, we assumed the proportion of the annual increment removed by hunting each year was 0.21 (SE = 0.05). The large standard error (25 percent of the mean) reflects the uncertainty associated with this parameter estimate. Population estimates based on pellet groups generally have low precision, and the error associated with the habitat suitability model for deer is compounded within its structural and functional components. In addition, hunting effort and success may differ widely owing to weather conditions.

The results of 10,000 simulations predicted a mean equilibrium ratio of 113 deer per wolf (SE = 29) (fig. 5a). A cumulative frequency plot of the results (fig. 5b) shows that there would be a 95-percent probability of equilibrium occurring if the ratio was 170 to 180 deer per wolf. Thus, if the objective is to maintain adequate prey to sustain 250 to 300 wolves on Prince of Wales and Kosciusko Islands (the current estimated population) with a 95-percent chance of equilibrium and still support subsistence and sport deer harvesting and current levels of wolf harvest, then sufficient habitat for 42,500 to 54,000 deer is needed. For comparative purposes, the habitat suitability model for deer (USDA Forest Service 1996) predicts the current habitat capability of Prince of Wales and Kosciusko Islands (on Federal lands) to be about 55,000 deer (margin of error unknown).

We caution that equilibrium does not necessarily imply stability, which is a measure of the tendency for a system to return to a condition of equilibrium after being perturbed (May 1974). Nonetheless, a large equilibrium ratio, particularly for wolves and deer confined to small geographic or habitat islands, would suggest a low probability of stability between predator and prey. The potential for equilibrium, and consequently stability, is diminished if habitat loss causes residual deer populations to exist at a

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[5] Alaska Department of Fish and Game. Unpublished data. On file with: Division of Wildlife Conservation, Douglas, AK 99824.

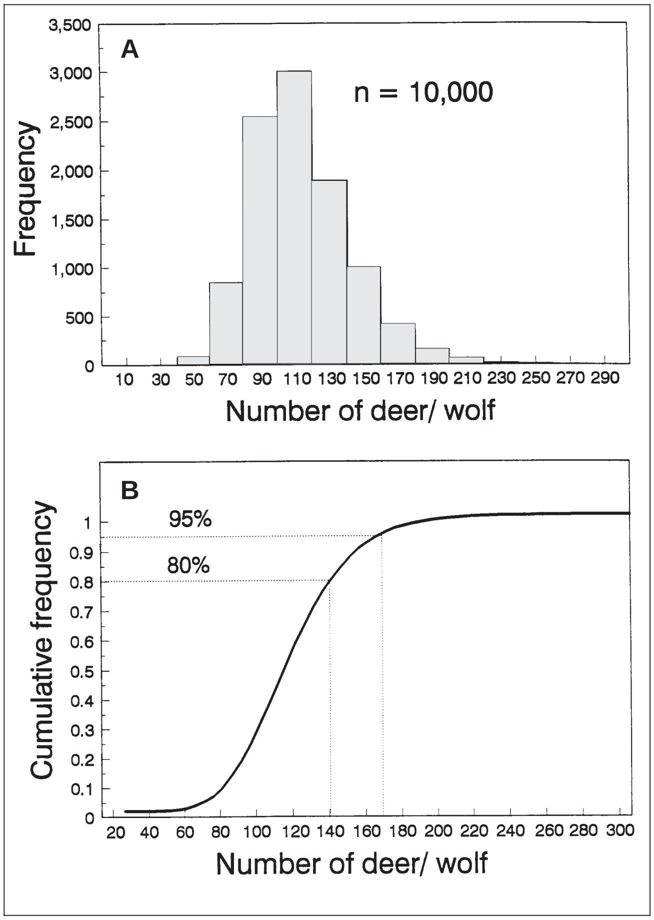

Figure 5—(**A**) Frequency plot of the number of deer per wolf (equilibrium ratio) predicted by Monte Carlo simulation of the equilibrium function. (**B**) Cumulative probability plot showing the number of deer per wolf needed for 80- and 95-percent probability of equilibrium.

lower density that is also closer to carrying capacity. Increased intraspecific competition for food within the remaining deer habitat will likely lower reproduction. For example, if λ were reduced to 1.15 and all other parameters remained the same, then the mean equilibrium ratio predicted by equation (9) is 219 deer per wolf (SE = 82). Over 380 deer per wolf would be needed for a 95-percent probability of equilibrium. The implication of this example is that equilibrium, and therefore stability, would be difficult to achieve and tenuous at best if carrying-capacity for deer declines.

Wolf Conservation

Our review raises a number of questions about the long-term viability and distribution of wolves in southeast Alaska. The Alexander Archipelago wolf exists in limited numbers in an insular environment undergoing rapid change. Issues focus on three general areas: (1) a decline in carrying capacity for deer; (2) the effect of road use by humans on mortality and displacement of wolves; and (3) continued exploitation of wolves. These changes are related to past and planned timber harvesting on Federal and private lands.

Prey Populations

Deer carrying capacity—Maintaining viable, well-distributed wolf populations ultimately will depend on maintaining habitat to support a relatively abundant, well-distributed, and stable population of deer. Short-rotation clearcut logging of old-growth forests in southeast Alaska will reduce habitat capability for Sitka black-tailed deer (USDA Forest Service 1991, 1996). This conclusion is supported by an extensive body of research spanning 30 years on forest succession following logging (Alaback 1982, Alaback and Herman 1988, Alaback and Juday 1989), silvicultural practices (Alaback and Tappeiner 1984, DellaSala et al. 1994, Doerr and Sandburg 1986, Nyberg et al. 1989), deer habitat relations (Bloom 1978, Kirchhoff and Schoen 1987, Klein 1964, Klein and Olson 1960, Schoen and Kirchhoff 1985, Schoen et al. 1988, Van Ballenberghe and Hanley 1984, Wallmo and Schoen 1980, Yeo and Peek 1992), and nutritional ecology of deer (Hanley 1984, 1987; Hanley and McKendrick 1985; Hanley et al. 1987, 1989; McArthur et al. 1993; Parker et al. 1993) in southeast Alaska. Short-rotation clearcut logging replaces productive old-growth forest, which is important deer winter habitat, with even-aged, second-growth stands of much lower habitat value for deer (Wallmo and Schoen 1980). Although young clearcuts may temporarily produce abundant forage, typically it is of poorer nutritional quality than forage available in old-growth forest stands (Hanley et al. 1989), and some understory plant species may never reappear on sites under short-rotation, even-aged management (Alaback 1982). Moreover, what forage is present is not available to deer during periods of deep snow.

Within 30 years of clearcutting, regenerating conifers shade out most understory vegetation (Alaback 1982), creating poor habitat conditions for deer (Wallmo and Schoen 1980). These stands represent a serious problem for deer because the habitat is poor in all seasons, and these conditions persist for a long time (150 to 200 years) (Alaback 1982, Wallmo and Schoen 1980). Although precommercial thinning may delay crown closure in second-growth stands, the improvements in their value as winter habitat for deer are modest and short-lived (<20 years) (Alaback and Tappeiner 1984).

Old-growth forest stands composed of relatively tall, large-canopied trees are particularly important to deer during severe winters. High-volume old growth intercepts snow more effectively than low-volume old growth (Kirchhoff and Schoen 1987) and receives disproportionately high use by deer during periods of deep snow (Schoen and Kirchhoff 1990). Under the current Forest plan (USDA Forest Service 1996, alt. 9), about 61 percent of the original productive old growth on Federal lands in GMU 2 will be cut within the next 100 years. About 15 to 20 percent of the land in GMU 2 is owned by Native corporations under the provisions of the Alaska Native Claims Settlement Act of 1971 (ANSCA). Between 65 and 81 percent of the original productive old growth on Native lands in GMU 2 will likely be cut within the next 20 years (USDA Forest Service 1991). Logging on both Federal and Native lands in GMU 2 will likely result in the conversion to young-growth forest of 75 to 80 percent of the original productive old-growth forest within 100 years. Timber harvesting on Federal and Native-owned lands in GMU 3 will remove about 48 to 50 percent of the original productive old-growth forest and, in combination with logging in GMU 2, will potentially affect over 65 percent of the wolf population in southeast Alaska (fig. 4).

This loss of habitat will likely reduce deer populations, and consequently affect deer-wolf dynamics. As our simulations have shown, habitat changes that lower reproductive rates in deer will reduce the probability of equilibria between wolves and deer and increase the sensitivity of equilibria to perturbation. In planning timber harvests, efforts to minimize the loss of long-term deer carrying-capacity at geographic scales consistent with the size of wolf pack home ranges, would likely reduce the probability of disequilibria between wolves and deer.

Forest fragmentation—In southeast Alaska, forests are a mosaic of high-, moderate-, and low-volume stands interspersed with open muskegs and alpine terrain. This natural fragmentation is intensified when clearcut logging converts individual forest stands into a patchwork of smaller old-growth stands isolated by clearcuts. During periods of deep snow, deer confined to isolated stands of old-growth forest consume the available food resources and suffer higher rates of mortality from malnutrition than deer in unfragmented old-growth forest (Kirchhoff 1994). If wolves also are present, then forest fragmentation may focus wolf predation on specific sites where deer are concentrated and relatively vulnerable (Hebert et al. 1982, Janz 1989, Nelson and Mech 1986b). For example, logging roads in southeast Alaska are typically constructed along the coastline or valley bottoms, with clearcuts spaced out along the roads on the lower hillsides. Residual patches of old-growth forest among clearcuts are connected by these roads, which are occasionally traveled by wolf packs. Deer concentrate in these patches during winter when snow depths prevent them from using open areas, and may suffer higher mortality from wolf predation.

From Vancouver Island, British Columbia, McNay and Voller (1995) report the efficiency of predation by wolves to be high in fragmented, heavily logged landscapes. They calculated the annual survival rate for adult resident deer at low elevations to be 73 percent and concluded this level, if continuous, is inadequate to sustain the deer population. In contrast, migratory deer, which made greater use of high-elevation habitats and completely avoided low-elevation second-growth forests in winter, were able to avoid predation and consequently had high rates of survival (95 percent). McNay and Voller (1995: 145) cautioned that:

> ...Retention of older, intact forests is basic to rebuilding deer populations. Forest harvesting, hence, road building and spatial isolation of winter habitats, may intensify predation on 1 segment of the deer population (resident deer) and indirectly impede recruitment to the other segment (migratory deer). The result likely contributes to declines in deer populations and an overall loss of population resiliency.

Avoiding further habitat fragmentation, especially at lower elevations and in the beach fringes where wolves commonly prey on deer in winter, should enhance the likelihood of maintaining deer populations in southeast Alaska. Alternative methods of timber harvest, such as single-tree selection could minimize the effects of logging, especially in areas of critical habitat for deer.

Roads

Studies in Wisconsin, Michigan, Ontario, and Minnesota indicate a strong relation between road density and the presence or absence of wolves (Fuller 1989, Jensen et al. 1986, Mech et al. 1988, Thiel 1985). These studies show that wolves generally failed to survive in areas with road densities >0.6 kilometer per square kilometer (0.9 mi/mi^2) whereas they persist in similar areas with lower densities of roads. Mech (1989) speculated that excessive mortality experienced by wolves in roaded areas is compensated for by individuals that disperse from adjacent roadless areas. Citing the expansion of wolf populations in Minnesota, Wisconsin, and Michigan, Mech (1995) suggested that road density is not really a deterrent, provided human populations

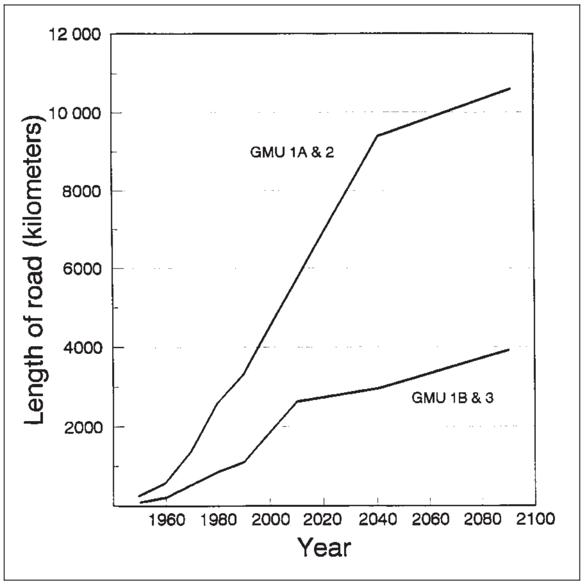

Figure 6—Kilometers of existing road and projections of future kilometers of road to 2090 for GMUs 1A, 1B, 2, and 3 (USDA Forest Service 1991). The GMUs encompass most of the range of wolves in southeast Alaska. The data do not include roads on state, private, or Native lands.

are tolerant of the presence of the wolves. Nevertheless, in an analysis of habitat selection by colonizing wolves, Mladenoff et al. (1995) report that roadless areas are preferred, and occupation of roaded landscapes occurs after roadless areas are saturated. In all the circumstances described in which wolves successfully inhabited roaded or developed areas, adjacent roadless areas were present.

There are several plausible explanations for the absence of wolves in densely roaded areas. In some instances, wolves may avoid roaded areas depending on the type of use the roads receive (Thurber et al. 1994). In most instances, their absence may be a direct result of mortality associated with roads (Berg and Kuehn 1982, Mech 1977, Van Ballenberghe et al. 1975). Substantial human-caused mortality can occur even when wolves are completely protected from legal hunting and trapping (Fritts and Mech 1981, Fuller 1989). Fuller (1989) reported that 80 percent of the identified mortality in a protected study area in Minnesota was human caused. Similarly, Mech (1989) noted that 60 percent of the mortality in a roaded study area was human caused, whereas no mortality was human caused in an adjacent roadless area.

Over the past 40 years, timber harvest has been most extensive in GMUs 2 and 3. Road densities in 50 percent of the Wildlife Analysis Areas (WAA) in GMU 2 and 17 percent of the Wildlife Analysis Areas in GMU 3 currently exceed 0.6-kilometer-per-square kilometer (USDA Forest Service 1996, Tongass land management plan geographic database), a density suggested to be inimical to wolves in other areas. The current Forest plan for the Tongass National Forest calls for road densities 3 to 4 times higher than exist today in GMUs 1A, 2, and 3 (fig. 6). Although wolves on Prince of Wales Island currently use areas with road densities greater than 0.6 kilometer per square kilometer (0.9 mi/mi^2), their “core areas” are generally located in the least densely roaded portion of the home range, and the wolf activity that does occur in densely roaded areas occurs primarily at night (Person, in prep.).

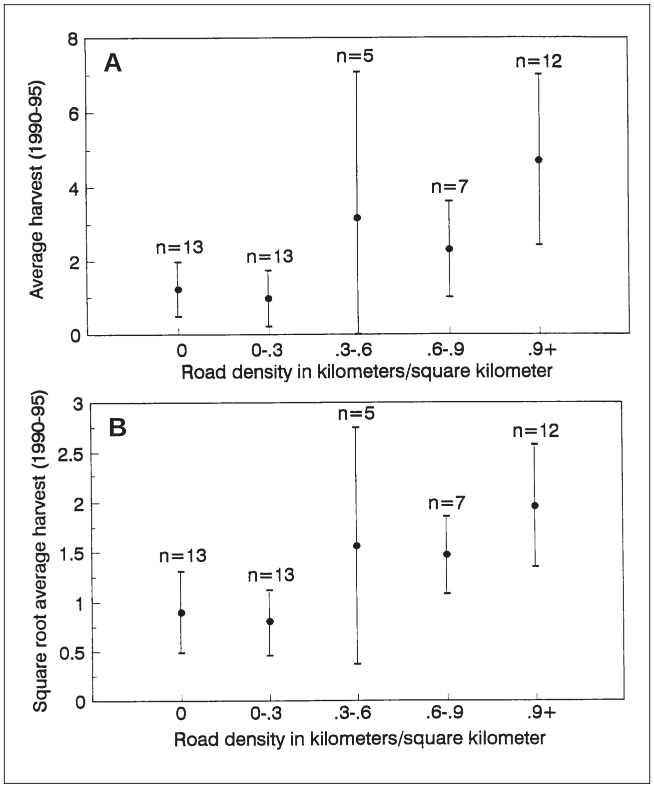

Figure 7—(A) Mean numbers of wolves killed per Wildlife Analysis Area (WAA) during the regular trapping and hunting seasons by the density of roads contained within a WAA after controlling for the size of the WAA. Harvest numbers represent the 6-year average harvest from 1990 to 1995. The filled circles represent the mean and the bars represent the 95-percent confidence intervals.

(B) Plot showing the mean number of wolves killed per Wildlife Analysis Area (WAA) during the regular trapping and hunting seasons by the density of roads contained within a WAA after controlling for the size of the WAA. Harvest numbers represent the square root of the 6-year average harvest from 1990 to 1995 to stabilize the variance. The filled circles represent the mean and the bars represent the 95-percent confidence intervals.

Based on harvest statistics from 1990 to 1995 in GMUs 2 and 3 and tabulated by WAA, wolves experienced significantly higher mortality from hunting and trapping in WAAs with higher road densities ($r = 0.59$, $P < 0.001$, $n = 56$). We calculated road density by using the area within a WAA below 370 meters (≈1,200 feet) elevation as the denominator. Wolves spend most of their time at low elevations (Person, in prep.), and calculations of road density should reflect this relation. Analysis of variance indicated a significant effect of road density on the 6-year average wolf harvest ($P < 0.002$, $df = 49$) reported for WAAs in GMUs 2 and 3 after controlling for the size of WAAs (a square root transformation of wolf harvest was used to stabilize the variance). Harvest rates increased sharply in WAAs exceeding 0.3 kilometer of road per square kilometer (0.49 mi/mi^2) (fig. 7a and 7b). Indeed, in two areas on Prince of Wales Island (Kasaan Peninsula and Big Salt Lake), trappers and hunters eliminated all known resident wolves (Person, in prep.). In both areas, road density exceeded 0.6 kilometer per square kilometer. Moreover, two female wolves with radio collars, each paired with a male, dispersed into the vacant areas and attempted to establish packs. Both wolves were killed (one legally, one illegally) by hunters within 18 months.

We regressed the 6-year (1990-95) average wolf harvest from WAAs in GMUs 2 and 3 against the linear kilometers of road within a WAA. To stabilize the variance, we used a square-root transformation of the harvest data for wolves. We used linear distance of road rather than road density, because most roads are along valley bottoms and through forest stands that are the most productive for timber and deer. Overall road density in a WAA may be low, but the roads that do exist are likely to go through or be located adjacent to areas used heavily by wolves.

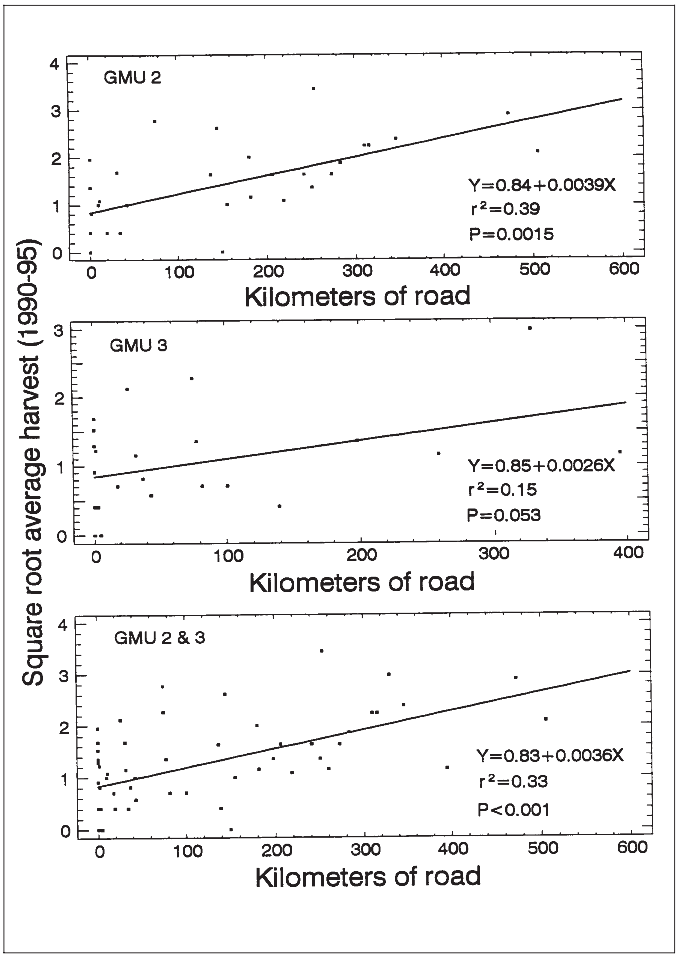

Figure 8—Plots showing regressions of the square root of the 6-year average wolf kill from 1990 to 1995 for GMUs 2, 3, and 2 and 3 combined versus the linear kilometers of road within a Wildlife Analysis Area (WAA).

Regression analysis indicated a significant positive relation between kilometers of road and wolf harvest (r^2 = 0.33 , *df* = 55, *P* < 0. 001) (fig. 8). The model predicted that wolf mortality due to hunting and trapping increased twofold when the linear distance of road exceeded 95 kilometers (59 mi), threefold when it exceeded 171 kilometers (106 miles), and fourfold when more than 234 kilometers (145 mi) of road existed within a WAA. The average area below 370 meters (≈1200 ft) in elevation for WAAs in GMUs 2 and 3 is 233 square kilometers; (89 mi^2); therefore, the distance values correspond to densities of road equivalent to 0.41, 0.73, and 1.0 kilometer per square kilometer, respectively (0.66, 1.19, and 1.63 mi/mi^2). We caution that the model explains only 33 percent of the variation in the data, and the hyperbolic prediction intervals around the regression lines are large; therefore, considerable deviation from predicted values is likely to be observed.

Means by which wolf mortality associated with roads can be better controlled would benefit from further investigation and consideration. This approach would include evaluating management of road use. For example, infrared traffic sensors and direct observations revealed that several roads posted as closed to motorized traffic on Prince of Wales Island were frequently driven over, and in two cases, gates were repeatedly vandalized in 1994 and 1995 to enable motorized access.[6] Further, the construction of gates or the removal of culverts may not be sufficient to eliminate all-terrain vehicle and snowmobile traffic.

Exploitation

Exploitation refers to the deliberate killing of wolves by people, either by trapping (and snaring) or shooting. For discussion purposes we divide the wolf kill into two categories, legal and illegal harvest. The legal harvest by hunters and trappers accounts for most of the annual take, and is typically managed by adjusting season lengths, harvest limits, or restrictions on methods of take. Illegal harvest includes wolves that are killed but are either not salvaged or otherwise not presented to ADFG for sealing of the pelts (as required by regulation). Illegal harvest is difficult to estimate, monitor, and control.

Legal and illegal exploitation of wolves will almost certainly increase as human populations increase, and as expanded access to the interior of islands brings people and wolves into more frequent contact. Furthermore, as human populations increase and the demand grows for a deer population that, under current habitat management, is simultaneously declining, wolves will inevitably be viewed by some as undesirable competitors. These trends in human population, access, and rates of exploitation are particularly evident on Prince of Wales Island. As recently as 1960, the human population on Prince of Wales Island numbered slightly more than 1,000 people. Air and ferry service were limited, and only a few kilometers of road existed outside a handful of small communities. Currently the population on the island and in the immediate area has grown to over 7,000 people (U.S. Department of Commerce 1996). The population has increased 13 percent since the 1990 census (U.S. Department of Commerce 1996). Since 1954, about 4,800 kilometers (3,000 miles) of road have been built on private and Federal lands on Prince of Wales Island.[7] [8] These roads, originally built for access to timber, now provide a transportation network among communities and provide people with ready access to many otherwise inaccessible areas of the island. This rapid rate of development is expected to continue. For the Ketchikan Area (GMUs 1A and 2), the kilometers of existing road will double in 30 years; the Stikine Area (GMUs 1B and 3) likely will have twice as many roads in 20 years (USDA Forest Service 1991).

Even though most of the wolves harvested in southeast Alaska are taken along the shore from boats (55 percent), a large and growing percentage are now taken from the road system (44 percent).[9] Roads on Prince of Wales Island access 19 of 22 Wildlife Analysis Areas, representing 78 percent of the land area in GMU 2. Except for the Thorne River area, all WAAs on the Island are accessible by skiff. Due to the relative ease of access and the continued efforts of trappers, wolves on Prince of Wales Island are heavily exploited. Total annual mortality on the island may exceed 45 percent (Person and Ingle 1995) in some years.

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[6] Person, D.K. Unpublished data. On file with the author.

[7] USDA Forest Service. GIS database. Tongass National Forest, Regional Office, Juneau, AK 99801.

[8] Alaska Department of Fish and Game. Internal report. 9 Feb. 1995. On file with: Habitat Division, Ketchikan, AK 99901.

[9] Alaska Department of Fish and Game. Unpublished data. On file with: Division of Widlife Conservation, Douglas, AK 99824.

Although trapping effort will undoubtedly diminish if wolf populations decline and animals become harder to catch, the relative ease of access and liberal hunting and trapping seasons may still result in harvest that is unsustainable. Deer populations currently may be sufficiently high to enable wolf numbers to rebound after several years of intensive trapping and hunting pressure. Nonetheless, if deer carrying capacity continues to decline in the future, then the resiliency of wolf populations likely will diminish, compounding the effects of overharvesting wolves by delaying or reducing the potential for their population recovery. In areas experiencing heavy mortality, regulatory changes may be needed to bring total wolf mortality within sustainable limits. Based on our analysis of birth rates and population size for wolves on Prince of Wales and Kosciusko Islands, we estimate the per capita birth rate for wolves to be approximately 0.33 (SE = 0.15). The buffering effects of immigration and emigration are probably limited for most of the wolves in southeast Alaska; consequently, total annual mortality should not exceed reproduction to maintain current population levels. Thus, to maintain current population levels, a level of mortality (from all causes; including natural, legal, and illegal harvest) for wolves in southeast Alaska is likely to be less than or equal to 30 to 35 percent.

Conclusions

Wolves, deer, and humans have coexisted in southeast Alaska for centuries and perhaps thousands of years. The natural environment of the past succeeded in supporting species that are of concern in the managed environment of the present. Given the overwhelming complexity of ecological systems and the state of scientific knowledge about them, we use the past as our default position, against which future management plans are compared. We suggest that the following questions be considered in making management decisions that may effect wolves and their habitat.

Can long-term deer carrying capacity be maintained at levels similar to current conditions after logging, particularly if clearcut logging is continued on a large scale?

This is the most important consideration for the long term. Results from research on postharvesting treatments of clearcut stands, such as precommercial thinning, suggest that benefits to deer from thinning are short-lived. The current state of knowledge offers no likely solutions to the problem of maintaining long-term deer carrying capacity while using extensive short-rotation clearcut logging. Other timber harvesting strategies, such as limited selection harvests, may ameliorate some of the impacts of logging on deer carrying capacity, but the effect of these alternative harvesting methods on deer is unknown at present.

If carrying capacity is reduced, then what is the minimum carrying capacity for deer that will support a viable and well-distributed population of wolves?

We cannot suggest a minimum deer population because we do not know what would constitute a minimum viable wolf population either demographically or genetically. Many more data are needed concerning the population structure, genetic structure, and predator-prey relations of wolves in southeast Alaska before this question can be answered. This question also must be addressed separately for the major island groups and possibly for individual sections of the mainland that are divided by major glaciers or river drainages. Our analyses suggest that sustaining the estimated current population of 250 to 300 wolves on Prince of Wales Island would require at least

42,500 to 54,000 deer (6 to 8 deer per square kilometer [16 to 21 deer/mi^2]) for a 95-percent probability of equilibrium. As deer carrying capacity declines in the years after extensive timber harvest, we would expect both deer numbers and reproductive rates to decline as well. In this situation, a disequilibria between wolves and deer likely would occur. Whether new equilibria would result is not known, but even if they do, they probably would be more difficult to achieve and less stable. At lower equilibria, there may be insufficient deer numbers to support current subsistence and sport deer harvest levels.

If roads are built, can access be managed effectively to reduce wolf mortality?

Effective management of roads to control human access should help to reduce wolf mortality; however, closing roads has not been fully successful because of practical difficulties and opposition voiced by residents within the communities affected by road closures. The demands of a growing human population for access to the Tongass National Forest for commercial and recreational purposes likely will make management of access even more difficult, while doing so will perhaps be even more important. A systematic access management approach that considers the biological requirements of wolves would be beneficial. For example, not building roads, or closing existing ones, in core activity areas or near denning sites would be beneficial. Of course, this type of action would require reliable information concerning the movements and activities of wolves in areas where access management is proposed. Considerable time and expense would be necessary to collect such information.

Can wolf mortality from trapping and hunting be controlled by regulatory changes?

Regulatory changes could have a marked effect on wolf mortality, nevertheless, the effect may be limited by the logistical difficulties of enforcing regulations in an area the size of the Tongass National Forest. Moreover, in areas where a large portion of the human population is employed in industrial or agricultural occupations, the number of wildlife law violations may be high (Berger and Daneke 1988). Educational programs concerning wolves, such as those available in Minnesota (International Wolf Center, Ely, MN), where a generation of people have grown up while wolves have been protected, might help the public understand the need to comply with regulatory changes in southeast Alaska and thus help to assure the effectiveness of regulations in managing human-caused mortality of wolves.

* * *

Although this report presents a substantial body of scientific information concerning wolves in southeast Alaska, the data are temporally and geographically limited in scope and caution must be used when drawing long-term, forest-wide conclusions from them. Nevertheless, we believe that continued extensive timber harvesting, especially short-rotation clearcut logging, will have adverse consequences for wolves and place some population segments at risk (particularly those wolves in GMU 2 and perhaps those in GMU 3).

In our opinion, the long-term consequences of continued short-rotation, clearcut timber harvesting and the short-term consequences of road access and legal or illegal wolf harvest result in increased risk to wolf viability. The Alexander Archipelago wolf exists as a population, perhaps less than 1,000 animals, that is potentially divided into smaller subgroups associated with different portions of the mainland and island clusters. Our analysis suggests that the largest portion of the population inhabits areas where extensive timber harvest has occurred or is planned. Maintaining a minimum average density of deer equal to 5 deer per square kilometer (13 deer/mi^2) in wildlife analysis areas that currently support deer numbers greater than or equal to 5 deer per square kilometer and where deer are the principal species of prey for wolves would reduce long-term risk to wolf viability. This density of deer is likely to support wolves and sustain the current subsistence harvest of deer by humans. In other wildlife analysis areas where deer are the primary prey, but current densities of deer are lower than 5 deer per square kilometer, maintaining deer numbers would reduce long-term risk to wolf viability.

In addition, in biogeographic provinces where extensive timber harvesting has occurred or where extensive harvesting is planned (see USDA Forest Service 1996 for description of biogeographic provinces), maintaining large, unfragmented, and unroaded blocks of habitat within each biogeographic province where wolves occur would reduce long-term risk to wolf viability. Making each “reserve” large enough to encompass the core activity areas of at least one wolf pack markedly increases the likelihood of their effectiveness. Core areas are often disjunct and the utilization distributions are frequently multimodal (Person, in prep.). Analysis of radio-telemetry data from wolves on Prince of Wales and Kosciusko Islands suggests that the 75-percent confidence ellipse (Jennrich and Turner 1969) or the 85-percent adaptive kernel home range (Worton 1989) would be adequate to delimit an area that completely overlaps core areas regardless of the shape of the utilization distribution (fig. 9). Both home range models indicate that risk to wolves increases if reserves are less than 200 square kilometers (78 mi^2) in size. An average density of 7 deer per square kilometer (18 deer/mi^2) has a high probability of sustaining 7 to 11 wolves (depending on the density of deer in the matrix that is overlapped by the wolf pack home range) of which 2 to 4 would likely disperse from the reserve annually. Given the high mortality rate for dispersers, we expect that at least one dispersing wolf would survive for more than one year and be available to replace wolves eliminated from the matrix.

Establishing at least one reserve per 800 square kilometers (≈300 mi^2) of area within each biogeographic province where wolves occur would meet the above need. The spacing of reserves is unlikely to be critical because wolves probably are highly mobile within provinces. The equilibrium model would predict that the proposed density of reserves would have a high probability of supporting about 30 wolves per 1000 square kilometers if the matrix of land between reserves can support a minimum of 5 deer per square kilometer.[10] Although the matrix of land

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[10] This density was computed as follows: no. of wolves supported by reserves + no. of wolves supported by matrix = ([200 × 7]/180)+[600 × 5]/80) = 24 wolves/800 square kilometers = 30 wolves/1000 square kilometers.

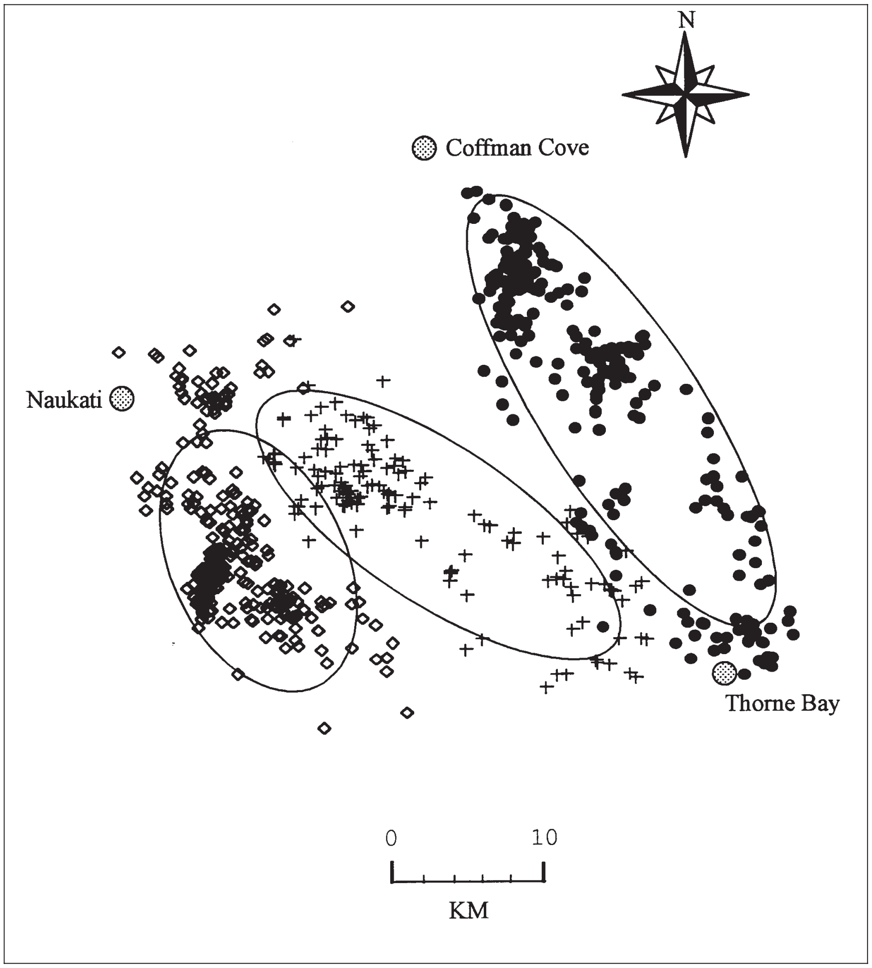

Figure 9—Radio locations for three wolf packs on central Prince of Wales Island, March 1993 to September 1995. The radio locations clearly indicate areas where activity is concentrated and illustrate the disjunct nature of the usage distributions. The area represented by the average of the 75-percent bivariate-normal confidence ellipse home ranges (shown) and the 85-percent adaptive kernel home ranges for all wolf packs monitored on Prince of Wales and Kosciusko Islands is suggested as the minimum size of reserves that will encompass the core activity areas of at least one wolf pack.

between reserves should be capable of sustaining wolves, the expectation is that the density of wolves in the matrix would be lower than in the reserves and individual packs may periodically disappear from these lands due to hunting and trapping (legal or illegal). The matrix of developed lands would presumably function as a wolf population sink siphoning off dispersers from the reserves, and thus increase the probability of stability between wolf and deer populations within the reserves. The matrix also would enable wolves to travel among reserves.

The objective of the reserves is to retain enough high-quality habitat with limited human access to assure that some packs persist as source populations for those wolves affected by extensive development. If the strategy described above was applied to Prince of Wales and Kosciusko Islands, then nine reserves would be created totaling about 180 000 hectares (437,000 acres). If timber harvest was limited and road construction prohibited in the reserves, consistent with reserve objectives, then risk to long-term wolf viability would be reduced. We predict that a total of 100 to 200 wolves would be sustained on Prince of Wales and Kosciusko Islands depending on the capability of the matrix to support deer over the long term and the intensity of human-caused mortality of wolves in the matrix.

We emphasize that this strategy is appropriate only for biogeographic provinces that currently support (or have the potential to support) dense populations of deer, such as those provinces within GMUs 2 and 3. Data are lacking concerning home ranges, movements, activity, and food habits of wolves inhabiting areas that can support only low densities of prey. Attempting to maintain the density of current prey populations and minimizing road construction would benefit wolf populations in these areas. More detailed and precise information should result from further research.

Acknowledgments

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Appendix 1

The model used to estimate the wolf population on Prince of Wales and Kosciusko Islands was as follows:

$$W_{pop} = \frac{A}{\left[H_R(1-\alpha)\right]} \bullet \frac{W_{pack}}{(1-\beta)}, \qquad (11)$$

where

W_{pop} = total wolf population,

A = area in square kilometers,

H_R = average home range in square kilometers,

α = proportion of home range overlapping neighboring wolf home ranges,

W_{pack} = average number of wolves per pack, and

β = proportion of dispersers in wolf population.

Parameter estimates used in the Monte Carlo simulation of the model were as follows:

1. Pack territories were calculated from empirical data (mean = 280 square kilometers [109 mi^2], SE = 78).[a]

2. Percentage of overlap among territories was calculated to approximate exclusive use areas by a single pack (mean = 0.04, SE = 0.01).

3. Pack sizes were estimated from aerial observations (mean = 9.0, SE = 2.6 in fall 1994; mean = 5.6, SD = 3.0 in spring 1995).[b]

4. Percentage of dispersers was determined from empirical data (mean = 0.29, SE = 0.09).

5. Land area of Prince of Wales and Kosciusko Islands is 6,808 square kilometers (2,654 mi^2).

The variance of the estimate is approximated by the following equation derived from the "delta" method (Seber 1983):

$$\begin{aligned}\text{Var } W_{pop} &= \text{Var}(H_R)\left[\frac{AW_{pack}}{H^2{}_R(\beta-1)(1-\alpha)}\right]^2 + \text{Var}(\alpha)\left[\frac{AW_{pack}}{H_R(1-\beta)(1-\alpha)}\right]^2 \qquad (12)\\ &+\text{Var } W_{pack}\left[\frac{A}{H_R(\beta-1)(\alpha-1)}\right]^2 + \text{Var}(\beta)\left[\frac{AW_{pack}}{H_R(\beta-1)(1-\alpha)}\right]^2\end{aligned}$$

The equation assumes that all variables are independent random samples with mean = μ and variance = α^2. Ten thousand simulations were conducted, each incorporating a random permutation of the input parameters.

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[a] The home range estimate is an average of MCP and 95-percent adaptive kernel home ranges.

[b] Pack size estimates include data from packs not containing radio-collared pack members.

Appendix 2

The Lotka-Leslie model used in this paper was derived in the following way. The formal model is expressed as:

$$l = \sum_{x=0}^{\infty} \frac{l_x b_x}{\lambda^x} \qquad (13)$$

where

l_x = survivorship to age class x,

b_x = number of female offspring per female of age x, and

λ = finite rate of increase assuming a stable-age distribution.

Recalling that $l_x = (s_{x-1})(s_{x-2})(s_{x-3})\ldots$,

where

s_x = annual survival rate for age class x,

the model can be rewritten as a function of survival rates:

$$1 = \frac{1(b_0)}{1} + \frac{s_0(b_1)}{\lambda} + \frac{s_0 s_1(b_2)}{\lambda^2} + \frac{s_0 s_1 s(b)}{\lambda^3} + \frac{s_0 s_1 s^2}{\lambda^4} + \ldots.$$

We assume that b and s for age classes >2 are constant. For wolves, $b_0 = b_1 = 0$, and b_2 represents the birth rate at age of first breeding, which is likely to be lower than the birth rate of older adults (b). Therefore the equation can be simplified as:

$$1 = \frac{s_0 s_1(b_2)}{\lambda^2} + \frac{s_0 s_1 s(b)}{\lambda^3}\left(1 + \frac{s}{\lambda} + \frac{s^2}{\lambda^2} + \ldots\right).$$

We then may solve for λ:

$$0 = \lambda^3 - s\lambda^2 - s_0 s_1 b_2 \lambda - s_0 s_1 s(b - b_2)\,. \qquad (14)$$

If we assume that $s_0 = s_1 = s$ and $b = b_2$ then the equation simplifies to:

$$\lambda = \frac{s + \left(s^2 + 4s^2 b\right)^{1/2}}{2}\,. \qquad (15)$$

The estimate of variance is obtained by the “delta” method described by Seber (1983):

$$\mathrm{Var}(\lambda) = \mathrm{Var}(s)\left(\frac{\partial\lambda}{\partial s}\right)^2 + \mathrm{Var}(b)\left(\frac{\partial\lambda}{\partial b}\right)^2,$$

which yields the following variance estimator:

$$\mathrm{Var}(\lambda) = \mathrm{Var}(s)\left(\frac{1 + 2b + \sqrt{4b+1}}{2}\right)^2 + \mathrm{Var}(b)\left(\frac{S^2}{4b+1}\right)^2. \qquad (16)$$

Survival rates were estimated from the survivorship of radio-collared wolves. The birth rate was estimated by the following formula:

$$b = \frac{f_p(1-\delta)}{f_{ad}}, \tag{17}$$

where

f_p = average number of female pups per pack (mean = 1.8, SE = 0.9),

δ = proportion of female dispersers in the female population (mean = 0.33, SE = (0.12), and

f_{ad} = average number of females per pack in spring (mean = 2.3, SE = 1.9).

The variance of the estimate was approximated by:

$$\text{Var}(b) = \text{Var}\ f_p\ \left(\frac{1-\delta}{f_{ad}}\right) + \text{Var}(f_{ad})\left(\frac{f_p(\delta-1)}{f^2{}_{ad}}\right)^2 + \text{Var}(\delta)\left(-\frac{f_p}{f_{ad}}\right)^2 . \tag{18}$$

Appendix 3

The wolf predation rate on Sitka black-tailed deer in southeast Alaska was calculated in the following way:

In southeast Alaska, adult bucks average 54.4 kilograms (120 lb; Merriam et al. 1994) and adult does average 42.2 kilograms (93 lb; Johnson 1987). Assuming a 60:40 female-to-male sex ratio in the adult population (due to buck-only hunting and higher natural mortality in males), the average adult deer weighs about 47 kilograms (104 lb; 42.2 kilograms × 0.6 plus 54.4 kilograms × 0.4). Winter fawns (<1 yr) average 19.5 kilograms (43 pounds; Johnson 1987). Predation rates on fawns versus adults are highly variable in the literature, and the factors affecting that ratio are poorly understood (Fuller 1989). We conservatively assumed that an average of one in three deer killed is a fawn (33 percent). About 74 percent of adult deer carcasses are consumed (Ballard et al. 1987, Fuller 1989) and 88 percent of fawn carcasses (Floyd et al. 1978). Thus, the average edible weight of each deer carcass is 29.1 kilograms or 64 pounds ([104 × 0.66 × 0.74]+[43 × 0.33 × 0.88]).

In other parts of North America where deer are the primary prey, the mean consumption rate of wolves is 0.04 kilogram of food per kilogram of wolf body weight (0.09 lb of food per pound of wolf body weight) per day (range 0.06 to 0.10; Fuller 1989). An average wolf on Prince of Wales Island weighs 30.4 kilograms (67 lb; *n*=26; Person, in prep.); thus, each wolf consumes 2.72 kilograms (6.0 lb) per wolf per day (0.09 × 67). Given that requirement, and assuming a diet composed 77 percent of deer, each wolf kills about 26 deer per year [(365 × 2.72 × 0.77)/29.1)].

Person, David K.; Kirchhoff, Matthew; Van Ballenberghe, Victor; Iverson, George C.; Grossman, Edward. 1996. The Alexander Archipelago wolf: a conservation assessment. Gen. Tech. Rep. PNW-GTR-384. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 42 p. (Shaw, Charles G., III, tech. coord.; Conservation and resource assessments for the Tongass land management plan revision).

We summarized the scientific information available for the Alexander Archipelago wolf (*Canis lupus ligoni*) in the Tongass National Forest of southeast Alaska. Information concerning the morphology, distribution, taxonomy, genetics, and ecology of wolves are presented. Three issues for the conservation of wolves in southeast Alaska are discussed: loss of long-term carrying capacity for deer due primarily to extensive timber harvesting, increased mortality of wolves associated with improved human access from roads, and continued high levels of harvest of wolves by humans. Continued timber harvesting at current levels and by current methods will likely have adverse consequences for some segments of the wolf population. Although some short-term regulatory changes and the management of road access may need to be considered to keep wolf harvest at a sustainable level, the most important consideration is to maintain long-term carrying capacity for deer, the principal prey for most of the wolf population. A series of old-growth forest reserves may provide an effective strategy to increase the likelihood that wolves will persist where extensive timber harvesting has occurred, or is planned.

Keywords: Alexander Archipelago wolf, *Canis lupus ligoni*, effects of logging on wildlife, population dynamics of wolves, predator-prey dynamics, roads and wolf mortality, Tongass National Forest, southeast Alaska.

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