ALEXANDER ARCHIPELAGO WOLVES: ECOLOGY AND POPULATION VIABILITY IN A DISTURBED, INSULAR LANDSCAPE

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ALEXANDER ARCHIPELAGO WOLVES: ECOLOGY AND POPULATION VIABILITY IN A DISTURBED, INSULAR LANDSCAPE

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ABSTRACT

The Alexander Archipelago wolf (*Canis lupus ligoni*) occupies Southeast Alaska, a region undergoing intensive harvest of timber. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) are the primary prey of these wolves. We conducted a telemetry study of 23 wolves on Prince of Wales and adjacent islands in Southeast Alaska between September 1992 and October 1995. We examined home range, habitat use, reproduction, mortality, and dispersal of wolves in logged landscapes and those that were relatively unlogged. We used those data to parameterize a wolf-deer model to predict long-term effects of timber harvest on the wolf-deer system on Prince of Wales and adjacent islands.

Home ranges of 7 wolf packs averaged 259 km^2 in winter but only 104 km^2 during pup-rearing season (15 April–15 August). Home-range size was positively correlated to pack size, and area per individual wolf was inversely related to the proportion of winter habitat for deer within the home range. Radiocollared wolves were classified as residents, extraterritorials, and dispersers. Annual mortality was 64% for extraterritorial and dispersing wolves and 31% for residents. Eighty-two percent of mortality was human caused. Radiocollared wolves were located mostly at low elevations (<250 m) regardless of time of year, and selected for old-growth forest habitat during pup-rearing season. Wolves generally avoided second-growth forests and clearcuts, and their use of those habitats occurred mostly at night. Density of roads was positively correlated with rate of harvest of wolves.

Simulations from our wolf-deer model indicated that deer and wolf populations on Prince of Wales and adjacent islands likely have declined since initiation of industrial-scale logging. Nonetheless, risk that the population of wolves will no longer be viable is low. Our predictions indicate that deer will decline disproportionately to decline of carrying capacity (*K*). Thus, a small change in *K* may precipitate large, long-term changes in deer numbers. The most important management strategy for the conservation of wolves in Southeast Alaska is to maintain high-quality habitat for deer. We believe that managing human access by closing roads for motorized use and limiting construction of new roads are also measures necessary to conserve wolves.

Key words: Alexander Archipelago wolves, black-tailed deer, *Canis lupus*, *Odocoileus hemionus*, population modeling, population viability, insular populations, predator-prey dynamics, southeastern Alaska, forest management.

NOTE ABOUT THIS COMPILATION OF *PERSON (2001)*:

This recompilation by Larry Edwards: (1) merges Figures and Tables (which formerly were in appendices) and Appendix A (entirely tables) into the body of the dissertation; (2) replaces the original (unreliable) Table of Contents, providing page numbers for the electronic PDF file – the numbers on the actual pages should be ignored; (3) provides PDF page numbers for the List of Figures and List of Tables; and (4) includes the page Recommendations signatures from a poor quality copy that was found in the Threemile project planning record.

The purpose of this recompilation is to have a handier desk reference.

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INTRODUCTION[1]

In their seminal work, MacArthur and Wilson (1967) proposed that theories of island biogeography could be applied to populations of a single species in addition to communities or guilds. Indeed, population viability analysis (PVA) is largely an application of theory from island biogeography to individual populations. Emphasis of PVA on single species has been useful for conservation of some threatened and endangered species; nonetheless, for obligate predators such as wolves (*Canis lupus*), viability of entire predator-prey systems must be considered rather than simply focusing on predator populations. This approach constitutes a partial reversion to the community perspective advocated originally by MacArthur and Wilson (1967).

To appreciate the importance of understanding predator-prey systems, especially with respect to conservation of wolves, consider that demographic parameters such as reproduction, mortality, dispersal, and immigration all are largely influenced by availability of ungulate prey (Packard and Mech 1980, Peterson et al. 1984, Ballard et al. 1987, Gese and Mech 1991, Boertje and Stephenson 1992). For example, if prey are abundant, wolves may compensate for high rates of harvest by increasing reproduction and survivorship of young (Ballard et al. 1987, Hayes 1995). Conversely, if prey abundance declines, dispersal rates and natural mortality will increase (Peterson and Page 1988, Gese and Mech 1991). Consequently, factors such as habitat loss that act on prey populations likely will have profound consequences for demographics of wolves.

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[1] This and all subsequent sections will be submitted as a single manuscript. Person, D. K., and R. T. Bowyer. *Prepared for submission*. Alexander Archipelago wolves: ecology and population viability in a

Extinction models commonly used to predict probability of persistence for a population over time generally relate some measure of maximum population size, or carrying capacity (*K*), to variance in birth and death processes caused by demographic and environmental stochasticity (Belovsky 1987, Gilpin 1987, Goodman 1987, Shaffer 1987, Boyce 1992). For wolves, *K* is a dynamic quantity related to availability of prey, thereby complicating predictions of probability that a population will persist. Further, ungulate prey often are shared with other consumers such as mountain lions (*Puma concolor*), bears (*Ursus* spp.), coyotes (*Canis latrans*) and humans. These elements in a predator-prey community are inextricably entwined with viability of wolf populations. In addition, scale and degree of isolation of predator-prey systems are important. Viability of a population of wolves occupying a large area without significant geographic barriers to dispersal or immigration may be buffered from effects of demographic and environmental stochasticity. In contrast, wolf populations confined to small patches of habitat or islands probably are more vulnerable to perturbations of a system if dispersal and immigration are restricted.

The Alexander Archipelago wolf (*Canis lupus ligoni*) is a relatively small gray wolf (generally <45 kg) that occupies the mainland and islands that compose the panhandle of Southeast Alaska (Goldman 1944, Pedersen 1982, Nowak 1983, Friis 1985; Person et al. 1996; Fig. 1). Person et al. (1996) estimated the population to be between 700 and 1,100 wolves in autumn 1995. Much of the region in encompassed by the 7-million ha Tongass National Forest, the largest national forest in the United States. During the past

50 years, timber harvesting on federal and adjacent private lands has resulted in clearcutting of approximately 411,000 ha of commercially valuable timberland (U. S. Forest Service 1997). Intensity of logging has been greatest in the southern portion of that region. For example, Prince of Wales Island, the largest in the archipelago and third largest in the United States, has had about one-third of all commercially valuable timber on federal and private lands clearcut, mostly since 1970 (U. S. Forest Service 1997, Alaska Department of Fish and Game GIS database). Prince of Wales and adjacent islands also support approximately one-third of the wolf population in Southeast Alaska (Person et al. 1996).

Timber harvest and associated development pose 3 potential problems for wolves: 1) loss of long-term carrying capacity for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), their principal prey, 2) high mortality of wolves because of human access provided by roads associated with logging activity, and 3) increased demand for harvest of deer and wolves by an increasing human population (Person et al. 1996). Conservation of wolves is complicated by the island topography of the region. At least on some islands, wolves likely exist as independent subpopulations with restricted migration and gene flow (Person et al. 1996). Consequently, these subpopulations may not be buffered by immigration or emigration and may be vulnerable to perturbations caused by human activity.

Our objective was to evaluate effects of timber harvesting and habitat change on wolves in Southeast Alaska. We focused on Prince of Wales and adjacent islands because those areas were logged most heavily and currently support a healthy

population of wolves (Person et al. 1996). Intensity of logging and accessibility of much of the area for human use could have far-reaching consequences for wolves. To assess those effects, we conducted a study of home-range characteristics, activity, habitat use, and demography of wolves, and then used those and other data to construct a model of the wolf-deer system. Our modeling not only accounted for "top-down effects of wolf predation on deer, but also incorporated "bottom-up effects of changes in habitat. Linking predator-prey dynamics with changes in habitat essential for deer provided a method to evaluate long-term consequences of timber harvest on wolves.

We focused the field portion of our study of wolves on exploring the following hypotheses that were relevant to our objective of constructing a habitat-based predator-prey model.

1) Pack and home range size are related to distribution and abundance of habitat for deer. Thus, home ranges should be smallest or pack sizes largest for wolves occupying habitat capable of supporting higher densities of prey (Peterson et al. 1984, Ballard et al. 1987). If correct, predictions about future abundance and distribution of wolves can be based on changes in habitat for Sitka black-tailed deer. This hypothesis is related directly to the notion that density of wolves is a function of prey biomass, a supposition that has considerable empirical support (Gasaway et al. 1983; Keith 1983; Fuller 1989; Gasaway et al. 1992; Van Ballenberghe and Ballard 1994; Messier 1994, 1995).

2) Wolves have been described as habitat generalists (Paradiso 1982), although few studies have examined habitat use by wolves. Mech (1995) suggested that most

habitats, even areas heavily modified by humans, are suitable for wolves provided human-caused mortality is limited. Nevertheless, wolves must have prey populations capable of sustaining them, and assuming that habitat important to populations of prey likewise will be significant for wolves is reasonable. Critical winter habitat for Sitka black-tailed deer in Southeast Alaska consists of closed-canopy old-growth forest on south- and

west-facing exposures <250 m in elevation (Wallmo and Schoen 1980, Schoen and Kirchhoff 1985, Schoen and Kirchhoff 1990). Those areas provide thermal cover and forage while minimizing accumulation of snow under the forest canopy (Wallmo and Schoen 1980, Kirchhoff and Schoen 1987, Schoen and Kirchhoff 1990). We predict that wolves will select critical habitat for Sitka black-tailed deer in winter. Deer should concentrate in those stands and selection of such areas by wolves would underscore the relation between habitat and deer, and their concomitant importance for wolves.

3) Roads that are built to facilitate harvesting of timber provide humans with access to most of the study area. Hunters and trappers use those roads to exploit wolves (Person et al. 1996). We predict that mortality of wolves from human causes will be related to density and distribution of roads. In the long term, roads may facilitate unsustainable rates of mortality caused by human exploitation concurrent with a decline in carrying capacity (K) for deer from clearcut logging. As a result, existence of wolf packs in some areas may become ephemeral, and presence of wolves in those areas would result from dispersal from adjacent, undeveloped lands.

4) Wolves are capable of long-distance dispersal (Fuller 1989, Gese and Mech 1991, Mech et al. 1998). Few data are available, however, concerning effects of large bodies of water on movements of wolves. We predict that dispersal from Prince of Wales and immediately adjacent islands to other island clusters or the mainland will be limited. Thus, population dynamics of wolves in the vicinity of Prince of Wales Island may be independent of other populations of wolves, indicating a patchy structure for the wolf population in Southeast Alaska, or possibly a metapopulation structure (Harrison et al. 1988, Taylor 1990).

In addition to testing the previous hypotheses, we combined demographic parameters estimated from field data, augmented by a literature review to construct a model of population dynamics of Sitka black-tailed deer and Alexander Archipelago wolves. Our model incorporates density-dependent patterns of growth in both predator and prey populations (Gilpin and Ayala 1973, McCullough 1979, Eberhardt 1998, McCullough 1987, McCullough 1999) and interactions of carrying capacity (K) of deer, road construction, exploitation of wolves, area, and geographic isolation. We tested our model against empirical data from Isle Royale, Michigan, and Southeast Alaska. We conducted simulations using scenarios that were consistent with current forest-management plans (U. S. Forest Service 1997) to predict long-term consequences of each scenario for the wolf population on Prince of Wales and nearby islands. We describe practical ramifications of our results for the conservation of wolves in Southeast Alaska, and discuss relevance of our work to other wolf-ungulate systems that exist in isolation and are influenced by human activities.

Effects of timber harvest on wolf populations likely will develop over many years or decades, and evaluating those effects is beyond the scope of a short-term field study. We believe that our approach of combining field study with population modeling is the only feasible strategy capable of addressing long-term consequences of forest management for wolves in a timely manner. Further, our model will provide a useful predictive tool for resource managers that can be refined as more data become available.

Background

In 1993, the Biodiversity Legal Defense Fund, an environmental organization based in Colorado, petitioned the U. S. Fish and Wildlife Service to list wolves in Southeast Alaska as threatened under the Endangered Species Act of 1973 (as amended). The petition cited overharvesting of wolves and effects of logging on populations of Sitka black-tailed deer as significant threats to wolves, particularly on Prince of Wales Island. The U. S. Fish and Wildlife Service ruled that a listing was not warranted, but that the petitioners had identified significant threats to wolves (U. S. Fish and Wildlife Service 1994). The petitioners successfully litigated that ruling, and the U. S. Fish and Wildlife Service was forced to re-evaluate their initial decision. During that process, the U. S. Forest Service revised the Tongass National Forest Land Management Plan (TLMP), which outlined the management direction for the next decade (U. S. Forest Service 1997). That revision established reserves of old-growth forest to provide habitat for wildlife species of concern, including Sitka black-tailed deer and wolves. TLMP also established some guidelines for managing human use of roads in sensitive areas for wildlife. In 1997, the U. S. Fish and Wildlife Service again ruled that the listing petition

was not warranted, citing provisions pertaining to wolves and deer in the revised version of TLMP as measures sufficient to maintain viable populations of wolves (U. S. Fish and Wildlife Service 1997).

In essence, TLMP is a massive experiment in adaptive management (Holling 1978, Szaro 1996). The plan assumes that a reserve strategy, reminiscent of the plan implemented in the Pacific Northwest for northern spotted owls (*Strix occidentalis*) (Thomas et al. 1990), is appropriate for species such as wolves. Although Person et al. (1996) suggested that a reserve strategy would reduce risk to wolves in areas that have been heavily logged, they did not conclude that such a strategy was sufficient to maintain viability of wolf populations.

Description of Alexander Archipelago Wolves.—Wolves in Southeast Alaska are generally smaller, coarser-haired, and darker in normal color than other wolves in Alaska and interior Canada (Goldman 1944, Wood 1990). Weights of adult males average 39.5 kg and adult females average 32.7 kg (Wood 1990). Wolves on Prince of Wales Island generally are smaller than average for the region (Person et al. 1996). Based primarily on skull morphology, Goldman (1944) concluded that wolves in Southeast Alaska constituted a subspecies distinct from other Alaskan and Canadian wolves and gave them the name "Alexander Archipelago wolf. Later taxonomic analyses suggested that *C. l. ligoni* was distinct from other Alaskan populations (Pedersen 1982), but grouped them with wolves that historically occupied the northwestern conterminous United States (*C. l. nubilus*; Nowak 1983, 1995). This classification is consistent with the hypothesis that wolves followed a postglacial

expansion of black-tailed deer northward into Southeast Alaska from southern coasts of British Columbia, Canada, and Washington (Klein 1965*a*).

Results from 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 Yukon, Canada (Shields 1995). In addition, genetic variation at 8 other nucleotides within mtDNA genomes of northern Alaska and Yukon wolves was not observed in any of the samples from Southeast Alaskan wolves. Genetic relations between *C. l. ligoni* and wolves from coastal and interior British Columbia, Montana, and Minnesota have not been investigated. Shields (1995) hypothesized that, based on the revised wolf taxonomy of Nowak (1995), the Alexander Archipelago wolf may show genetic affinity with historic wolf populations from coastal British Columbia and Vancouver Island, Canada.

Distribution and Abundance.—Wolves occur on the strip of mainland between Yakutat Bay in the north to Dixon Entrance in the south, and on islands south of Frederick Sound (Fig. 1). Immigration and emigration are restricted to several river drainages that penetrate the Coast Mountains to the east and connect the region to interior British Columbia and the Yukon. Some dispersal of wolves may occur in the south along the coast of British Columbia, but mountains and extensive glaciation likely prohibit dispersal in the northern part of that region. The total population of wolves in the archipelago and on the mainland probably numbers <1,000 animals, and may be divided into smaller subpopulations associated with portions of the mainland and different clusters of islands (Person et al. 1996). Sitka black-tailed deer are the principal

Figure 1. Southeast Alaska, USA, showing game management units 1–5 designated by the Alaska Department of Fish and Game.

prey of wolves (Smith et al. 1987, Kohira 1995, Kohira and Rexstad 1997), and wolves are most abundant (>30 wolves/1,000 km^2) in areas that contain the best habitat for deer (Person et al. 1996).

Concerns for the Conservation of Wolves.—Analysis of wolf feces (n = 545) from Prince of Wales and Revillagigedo islands (Fig. 2) suggested that about 77% (SE = 10%) of the diet was composed of Sitka black-tailed deer (Person et al. 1996). Feces used for that analysis were collected during periods when numbers of deer were considered to be moderate for the region (Alaska Department of Fish and Game 1996). Beaver (*Castor canadensis*) composed only 13.7% (SE = 9%) of the diet, and all other species contributed <10%. In areas of the mainland where deer are scarce, important prey include beaver, mountain goat (*Oreamnos americanus*), and moose (*Alces alces*) (Smith et al. 1986*a*, Wood 1990). Wolves in Southeast Alaska have access to spawning salmon (*Onchorynchus* spp.) during late summer and early autumn (Smith et al. 1986*b*, Wood 1990, Kohira 1995, Kohira and Rexstad 1997, Szepanski et al. 1999). Wolves also feed opportunistically on harbor seals (*Phoca vitulina*), mustelids including river otters (*Lontra canadensis*), small mammals, birds, and marine invertebrates (Garceau 1960, Merriam 1966, 1968, Smith et al. 1986*b*, Kohira and Rexstad 1997).

Sitka black-tailed deer in Southeast Alaska are near the northern extremity of their distribution and, therefore, are particularly vulnerable to excessive accumulation of snow in winter (Wallmo 1981, Schoen and Kirchhoff 1985). Critical habitat for deer in winter is characterized by elevations <250 m, south or west-facing slopes, and high-volume old-growth forest. The uneven-aged stratification of this old-growth forest

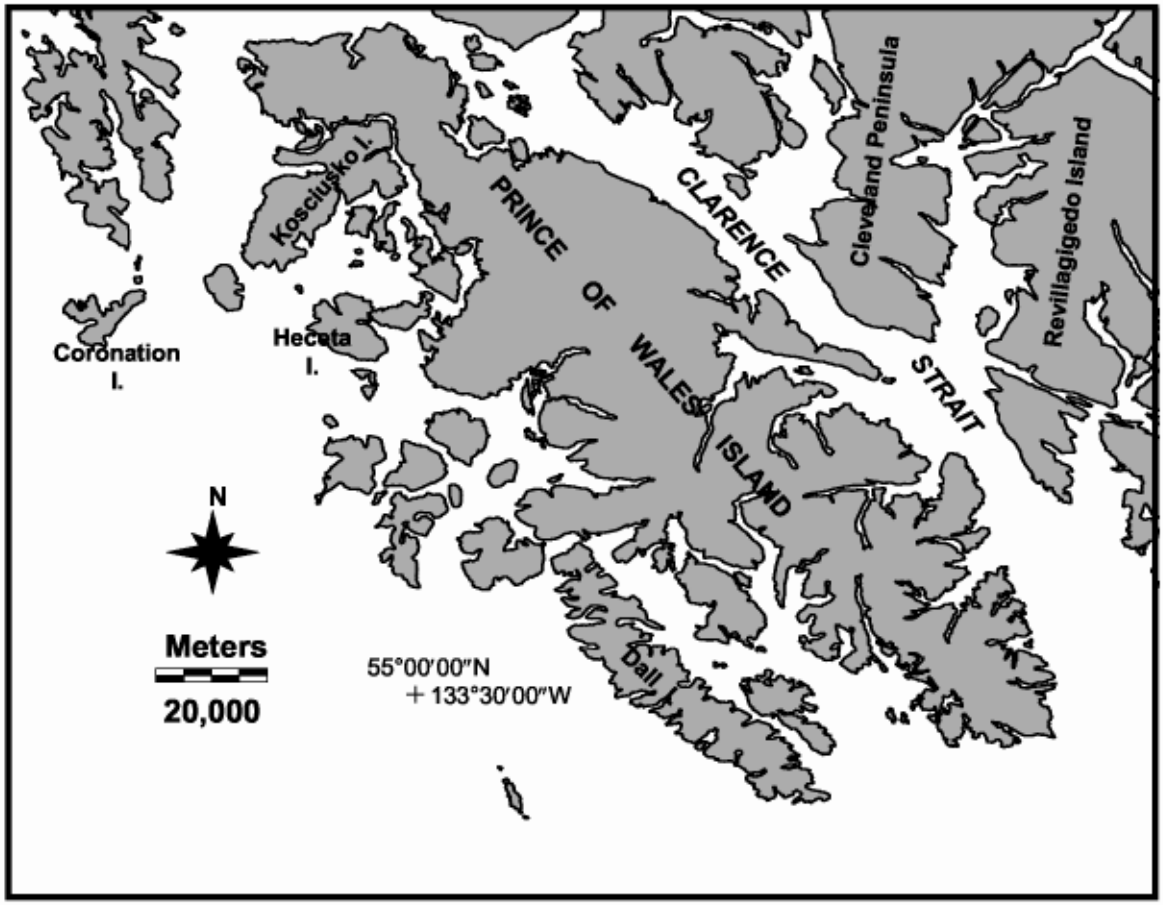

Figure 2. Prince of Wales and adjacent Islands in Southeast Alaska, USA. Research primarily focused on wolves located on the north-central portion of Prince of Wales Island and on Kosciusko Island.

provides a dense overstory canopy that intercepts snow, yet allows sufficient light to reach the forest floor to enable growth of forage for deer that is available year-round. In contrast, clearcuts (the dominant timber harvesting regime) provide abundant forage for 25–30 years, but shrubs and herbaceous vegetation (forbs) are not available to deer during winters with substantial (>25 cm) snowfall (Wallmo and Schoen 1980, Parker et al. 1984). Although quantity of forage available in clearcuts in early successional stages is high, that forage is of poorer nutritional quality than forbs and shrubs growing in old-growth stands (Hanley and McKendrick 1983, Hanley 1984, Hanley 1987, Hanley et al. 1987, Hanley and Spalinger 1989, Hanley and Rogers 1989). After 25-30 years, clearcuts grow into a "stem-exclusion or seral-forest stage, in which the dense canopy prevents sunlight from reaching the forest floor and eliminates forage for deer (Wallmo and Schoen 1980, Alaback 1982). That stage lasts from 150-200 years before old-growth structure may begin to return to the stand (Wallmo and Schoen 1980). Although silvicultural practices, such as pre-commercial thinning, may delay canopy closure in seral stands, effects are short-lived and residual slash retards forage production for several years after thinning (Della Salla et al. 1994).

Winter weather affects population dynamics of deer in Southeast Alaska (Klein and Olson 1960, Klein 1965*b*, Olson 1979, Schoen and Kirchhoff 1985) and can have significant effects on rate of predation by wolves (Hoskinson and Mech 1976, Mech and Karns 1977). Nevertheless, resiliency of deer to effects of winter and wolf predation is likely a function of ecological carrying capacity (*K*) for deer (McCullough 1979, 1987, 1999) and distribution of deer with respect to wolves (Hoskinson and Mech 1976).

Further, hunting of deer by humans and intensity of harvesting of wolves also will contribute to the ability of deer to rebound after declines from severe weather in winter. In places where winter habitat for deer has been degraded, and long-term *K* carrying capacity diminished because of timber harvesting, deer could be more susceptible to winter weather (Bowyer et al. 2000). In addition, deer living in landscapes where timber harvesting is widespread may produce fewer recruits, thereby making the population less resilient to predation by wolves, bears, and humans (Van Ballenberghe and Hanley 1984). Under those circumstances, declines in populations of deer and their suppression by predation and hunting may occur even after relatively mild winters.

About 6,500 km of roads currently exist within the Tongass National Forest of which more than one-half are on Prince of Wales Island. Although roads do not pose a direct hazard to wolves (Mech 1995), they provide access to wolf habitat by humans intending to hunt or trap wolves either legally or illegally. Roads tend to occur at elevations <250 m and access high-volume stands of old-growth timber that represent critical habitat for deer in winter as well as areas frequented by wolves in search of prey. Person et al. (1996) showed that there was a significant relation between kilometers of road and rate of harvest of wolves within watersheds on the most extensively logged islands in Southeast Alaska. Approximately 12,000 km of roads are planned to be built in the Tongass National Forest by 2045 (U. S. Forest Service 1997).

Wolves were subject to predator control measures, including bounties and poisoning during the 1950s and 1960s (Lesink 1959, Harbo and Deane 1983). Annual harvests of wolves in Southeast Alaska averaged 107 (SE = 45) animals between 1950

and 1969 (Alaska Department of Fish and Game unpublished data). Government-sponsored efforts at wolf control dwindled in the 1970s and ceased altogether in 1976. Wolves are currently harvested during hunting and trapping seasons that are regulated by the Federal Subsistence Board and the Alaska Board of Game. In most areas, the hunting season extends from 1 August to 30 April with a harvest limit of 5 wolves/hunter; the trapping season starts 10 November and ends 30 April with no limit on harvest. In Game Management Unit 2, which includes Prince of Wales Island (Fig. 1), the hunting season begins on 1 December and ends 31 December with a bag limit of 5 wolves. The trapping season begins 1 December and ends 31 March, with total harvest limited to 30% of the population. Human demand for deer combined with loss of *K* may place wolves in direct conflict with humans where timber harvesting has been extensive. An increasing human population (Bureau of the Census 1999) likely will heighten demand for deer and lead to intensified management of wolf populations.

STUDY AREA

Southeast Alaska comprises a narrow strip of mainland and a chain of islands, the Alexander Archipelago, which is oriented roughly parallel to the mainland (Fig. 1). The archipelago consists of thousands of islands ranging in size from <0.01 to 6,335 km^2, with distances between islands and the mainland ranging from several meters to 13–15 km. Several river drainages penetrate the Coast Range Mountains of the mainland and connect the region to interior British Columbia and the Yukon Territory, Canada. Weather conditions are highly variable, with annual precipitation ranging between 130 and 400 cm (National Weather Service 1998). Accumulation of snow is greatest on the

mainland and northernmost islands and becomes intermittent in the southern portion of the archipelago. Generally, the further west an island is situated from the mainland, and the further south within the archipelago, the more maritime the climate, resulting in warmer, wetter weather, but less accumulation of snow. Nonetheless, accumulations of snow may be high on islands with extensive mountain systems regardless of their position relative to the mainland.

Our study area encompassed 4,014 km^2 located on north-central Prince of Wales Island, Kosciusko Island, and all of the smaller islands within Sea Otter Sound, including Heceta Island (between 55° 25′ and 56° 15′ N, and 132° 30′ and 133° 50′ W, Fig. 2). The area constitutes a portion of game management unit 2 of the Alaska Department of Fish and Game. Game management unit 2 is subdivided into wildlife analysis areas, which generally represent individual watersheds. Prince of Wales Island is 6,335 km^2 and Kosciusko Island encompasses 473 km^2. Other islands range from <0.005 to 180 km^2. Rugged mountains extend to 1,160 m in elevation, and long deep fiords characterize the shoreline.

Elevations <800 m are covered by temperate rainforests of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Alaska cedar (*Chamaecyparis nootkatensis*), interspersed with muskeg bogs dominated by sparse stands of shore pine (*Pinus contorta* var. *contorta*) and sphagnum mosses (*Sphagnum* spp.). Subalpine and alpine vegetation, including partridgefoot (*Luetka pectinata*), deer cabbage (*Fauria crista-galli*), and heather (*Cassiope* spp.), exist above 800 m, with highest elevations covered by rock and ice. Common understory

shrubs include several species of blueberry (*Vaccinium* spp.), rusty menzesia (*Menzesia ferruginea*), salmonberry (*Rubus spectablis*), and devil's club (*Oplopanax horridus*). Alaback (1982) and Alaback and Juday (1989) describe understory characteristics and ecology of these forests in greater detail.

About 120,000 ha have been clearcut logged on Prince of Wales and adjacent islands (U. S. Forest Service 1997, Alaska Department of Fish and Game GIS database). In addition, >4,800 km of roads ($\bar{x}$ = 0.7 km/km^2) have been built on federal, state, and private lands. Within the study area, 92,332 ha have been logged and 2,657 km of roads have been built since 1955.

Mammals commonly occurring within the study area other than wolves and Sitka black-tailed deer include black bears (*Ursus americanus*), beaver, river otters, other mustelids, and several species of small rodents (*Glaucomys sabrinus, Peromyscus keeni, and Microtus longicaudus*). In addition, Steller sea lions (*Eumetopias jubatus*) and harbor seals occur in marine waters and are occasionally available to wolves as carrion along beaches. Spruce grouse (*Dendragapus canadensis*) inhabit forested habitat and a variety of waterfowl (Anatidae) are seasonally abundant in estuaries and along the shorelines. Most major streams and rivers support several species of salmon and annual spawning occurs between June and October.

METHODS

Capture and Immobilization of Wolves

The field portion of our research was conducted between October 1992 and October 1995. We used #14 Newhouse leghold traps to capture wolves. Traps were examined

daily and wolves that were captured were immobilized with intermuscular injections of Telazol® (5-6 mg/kg; Wildlife Pharmaceuticals, Fort Dodge, Colorado) administered from either a blowgun or a pole syringe. Wolves were weighed using a hanging scale, and standard measurements, including total length and heart girth, were taken. We fitted each animal with a radiocollar (Telonics, Mesa, Arizona) containing a mortality sensor with a 12-hr delay and released it. Each radiocollar had a battery life of 36 months. All methods used to capture and handle wolves were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks, and were in keeping with guidelines set forth by the American Society of Mammologists (Animal Care and Use Committee 1998).

We captured and radiocollared 24 wolves from February 1993 to November 1994. About 4,700 trap nights were expended with an average of 196 trap nights required to capture each wolf. Our rate of capture was 1 wolf /11 days. We initially attempted to capture wolves anywhere within the study area. Nonetheless, once we successfully radiocollared wolves from a particular pack, we subsequently concentrated on capturing wolves from adjacent packs. That strategy enabled us to evaluate overlap between pack home ranges. Five adult females, 6 adult males, 6 yearling females, 1 yearling male, 2 juvenile females, and 4 juvenile males were radiocollared. One adult female died within 1 month of capture; we attribute her death to malnutrition resulting from an injury to her foot caused by the trap. That particular female was captured by a local trapper who donated the wolf to our research project, and infection subsequent to her capture may have contributed to her death. No other capture-related mortalities occurred among

those wolves fitted with transmitters and released. Nonetheless, 4 other wolves died during capture. A juvenile female was euthanized because of a severe injury to 1 of her rear legs caused by the trap. That animal was caught in an unmodified version of the #14 Newhouse trap. After her capture, we determined that the offset width of our traps was insufficient to prevent such injuries. Thereafter, we fitted each trap with cable clamps placed within the jaws that increased the trap offset from 9.5 to 18 mm. This modification eliminated other serious trap-related injuries. Another juvenile female died in 1 of our traps. Examination of the carcass revealed that she had been attacked and bitten by other wolves. The trap site was near the border between 2 wolf packs, and we believe that she was attacked by wolves from the neighboring pack. In addition, 1 juvenile male was shot in 1 of our traps by persons who were driving by the site. The road on which the trap was set was closed to vehicular traffic, and the individuals involved were illegally driving on it. Similarly, another wolf was stolen from our trap by individuals who were illegally driving on a closed road.

Telemetry

Radiocollared wolves were tracked aerially and from the ground. Locations of wolves obtained from the ground were determined by triangulation from at least 2 azimuths. All locations were judged to be either good or poor quality, depending on signal strength and directionality. Most locations (≈ 90%) were obtained by a single observer and the median time lag between azimuths was 6 min (interquartile range = 5 min). Approximately 10% of locations involved 2 observers simultaneously recording bearings. Coordinates of each radio location obtained from fixed-winged aircraft were

determined by nondifferentially corrected GPS calibrated for the 1927 North American datum for Alaska; those locations were truthed against geographically referenced orthophotographs. Positions of ground-based telemetry stations were determined by nondifferentially corrected handheld GPS. We were unable to use orthophotos to truth positions of most telemetry stations because the photographic series available for the region showed few roads that we used. Accuracy and precision of the GPS unit was determined against surveyed benchmarks and had a SE = 32 m. Thus, 95% of GPS locations for telemetry stations were probably within 64 m of the true position. Data for radio locations and telemetry stations were recorded as Universal Transverse Mercator (UTM) coordinates.

Accuracy and precision of radiotelemetry locations were determined by periodically testing observers by placing radiocollars at known locations. Aerial locations were within a radius of 100 m of true locations. Precision of ground-based telemetry bearings was ±4° for good-quality signals and ±9° for poor signals. For a good-quality signal, ground-based locations generally were within a distance of 100 m from the true location, and poor-quality signals were within 350 m of the true location. We deleted all ground-based radio locations in which any telemetry station was >4,000 m from the estimated location of the wolf. Median distance of telemetry stations from estimated locations of wolves was 435 m (interquartile range = 1,364 m).

We located our study animals aerially once or twice each month depending on weather conditions. In addition, each wolf was located at least once per week from the ground. We used a randomized time schedule between 0 and 23 hr for collecting radio

locations from the ground. Snowfall in late autumn and winter often made roads impassable and limited our ability to conduct ground-based telemetry. As a result, we could not obtain as many nighttime locations in winter as we planned, even though hours of darkness were long. Long hours of daylight during late spring, summer, and early autumn enabled us to obtain many locations during daylight but few at night. As a result, only 385 (26%) radio locations were recorded during night and 1,103 (74%) during daylight.

Estimating Home Range

Tests of serial correlation.—Effects of spatial autocorrelation on analysis of home range and habitat use have been debated extensively (Swihart and Slade 1985, White and Garrott 1990, Swihart and Slade 1997). All territorial animals likely exhibit spatially correlated movements to some degree and this needed to be addressed before applying statistical analyses that assume spatial independence in data. We reduced effects of serial correlation by maintaining a minimum interval of 24 hr between locations for each wolf. We tested for significant correlations ($P \leq 0.05$) between successive radio locations for each animal by using autocorrelation functions for X and Y coordinates and a cross-correlation function for X versus Y coordinates (Person and Hirth 1991). If spatial correlation was significant among successive radio locations for a particular wolf, we selected an uncorrelated random subset of those data for use in analyses that required an assumption of spatial independence such as analysis of habitat use.

Home-range models.—We used Mohr's convex polygon (MCP) and 95% adaptive kernel (ADK; Worton 1989, Kie et al. 1996) models to estimate home ranges for individual wolves and for packs. Ninety-five percent ADK home ranges were presented for comparison with MCP home ranges, but were not used in other analyses. We used 50% ADK home ranges to define areas of intense activity. Home ranges of wolf packs were estimated by combining data from all radiocollared wolves within a pack. We estimated home ranges for the pup-rearing season (15 April–15 August) for each pack and compared those values with home ranges derived from locations obtained outside that period. Using area-observation curves (Odum and Kunzler 1955, Person and Hirth 1991), we determined that a minimum of 30 radio locations per season was necessary to estimate home ranges for wolves.

Estimating Demographic Parameters

Reproduction and mortality.—Radiocollared wolves enabled us to locate active dens for all wolf packs monitored in May and June. In addition, active dens of other packs within the study area were located opportunistically by U. S. Forest Service personnel while conducting wildlife and timber surveys. During pup-rearing seasons in 1993 and 1994, we attempted to estimate sizes of litters by observing active dens from a distance with spotting scopes. Dense understory vegetation near dens made that approach difficult and unreliable. In 1995, we visited each active den in late May or early June and estimate minimum sizes of litters by counting young observed in or near the den. That method enabled us to estimate sizes of litters at 6 den sites. Only 1 wolf pack moved pups to an alternate den after we visited the site.

Activity of wolves during radio tracking was categorized as moving, resting, dead, or unknown. Movement was determined by signal modulation and sequential monitoring (Person and Hirth 1991). Radiocollared wolves were monitored at least once per week for signals indicating mortality. Mortalities were investigated as soon as possible after detection (usually within 1–2 days). Carcasses were examined for cause of death and location and habitat were recorded. We supplemented data on mortality of radiocollared wolves with unpublished data on the harvest of wolves within wildlife analysis areas provided by the Alaska Department of Fish and Game to examine the effects of habitat and roads on mortality and rates of harvest of wolves.

Dispersal and extraterritorial movements.—We defined 3 social classes of wolves: dispersers, extraterritorials, and residents (Fritts and Mech 1981, Van Ballenberghe et al. 1975, Gese and Mech 1991). Residents were pack members that remained within pack home ranges and were observed interacting with other pack members. Extraterritorial wolves remained on the fringe of resident packs but had well-established home ranges. Dispersers were wolves that made determined movements away from resident packs and did not return. Dispersing wolves were tracked until they died or established new home ranges.

Pack size.—Pack size was determined by aerially locating packs with radiocollared individuals and counting their numbers (Fuller 1989, Gasaway et. al. 1992, Dale et al. 1994). Estimates of pack size were made in autumn and again in spring.

Habitat Use

Characterizing habitat.—We defined the following habitat types: alpine, lakes and streams, open-canopy old-growth forest, closed-canopy old-growth forest, clearcut, closed-canopy second-growth forest, unspecified private lands, and roads (Fig. 3). These classifications are known to be biologically important to deer in Southeast Alaska (Wallmo and Schoen 1980, Schoen and Kirchhoff 1990) and also should be significant to wolves.

Alpine habitat is nonforested land above 660 m. This habitat is characterized by rugged, open terrain covered with low herbaceous vegetation. Abundance and quality of forage for deer is high and a large portion of the deer population migrates to alpine habitat during summer (Schoen and Kirchhoff 1985, McNay and Voller 1995). In winter, deep snow forces deer to migrate to lower elevations.

Frozen lakes and streams may be used as travel corridors by wolves as well as places to corner or trap and kill deer. In summer, salmon spawning may attract wolves to streams and lakes.

Open-canopy old-growth forest is characterized by interspersion of open muskegs (bog-like areas sometimes containing floating mats of mosses) and stands of old-growth forest containing small basal areas (Ω15,000 bf/acre; 87.4 m^3/ha). In forested areas, the canopy is relatively open and understory vegetation is profuse. These areas provide good habitat for deer during snow-free months. Nonetheless, in winter the open canopy allows snow to accumulate on the forest floor, covering forage and impeding movements of deer (Wallmo and Schoen 1980, Kirchhoff and Schoen 1987).

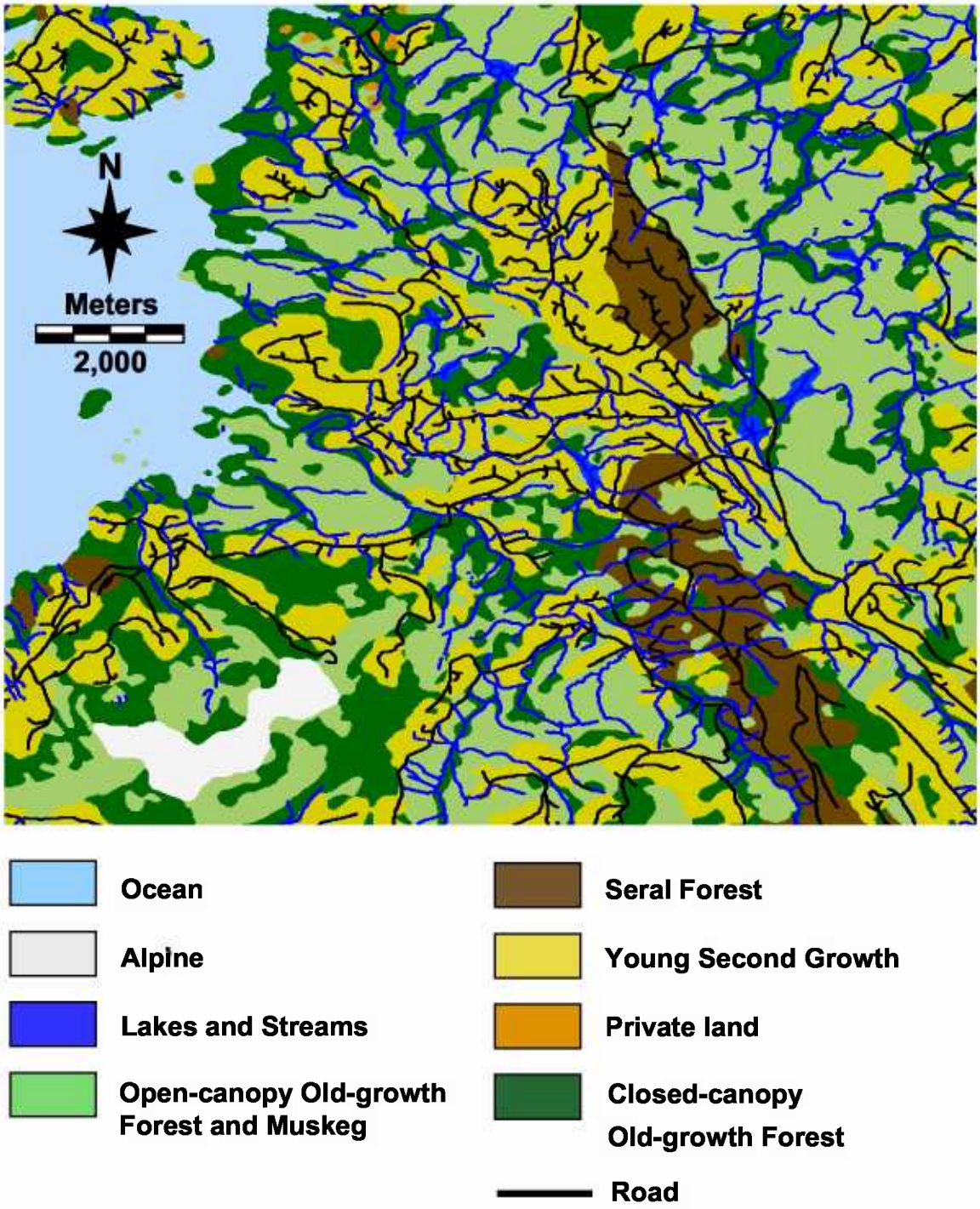

Figure 3. Portion of the study area on Prince of Wales Island, Southeast Alaska, USA illustrating habitat classifications used in analysis of habitat use by wolves.

Closed-canopy old-growth forest are stands that have relatively high basal areas of timber (>15,000 bf/acre; 87.4 m^3/ha) that are of uneven age. The forest canopy is patchy allowing sunlight to reach the forest floor yet it still intercepts snow. Understory vegetation is abundant and nutritional quality for deer is high (Alaback 1982, Hanley and Rogers 1989, Parker et al. 1999). Closed-canopy old-growth forest provides good quality habitat for deer in all seasons. This habitat is particularly important in winter when deep snow is present in habitats with open canopies (Wallmo and Schoen 1980, Kirchhoff and Schoen 1987, Schoen Kirchhoff 1990, Parker et al. 1999). We defined critical winter habitat for Sitka black-tailed deer as closed-canopy old-growth forest <250 m elevation and on aspects from 135–225° (Wallmo and Schoen 1980, Schoen and Kirchhoff 1985, Schoen and Kirchhoff 1990; Fig. 4).

Management of even-aged forests is the dominant silvicultural strategy within the study area (U.S. Forest Service 1997). Clearcut logging completely removes the forest canopy and leaves behind large quantities of untreated slash (U. S. Forest Service 1997). Natural regeneration of spruce and hemlock becomes noticeable after 5 years, and young clearcuts generally produce an abundance of woody browse, particularly *Vaccinium* (Alaback 1982, Schoen et al. 1988). After 20–30 years, the canopy of regenerating spruce and hemlock closes over and shades out understory vegetation (Wallmo and Schoen 1980, Alaback 1982). We defined clearcuts as second-growth habitat ≤25 years old, and seral forest as second-growth habitat >25 years old. The division represents a breakpoint between second-growth forest that provides forage for deer and those areas with little understory vegetation. Clearcuts are used seasonally by deer, but wolves may

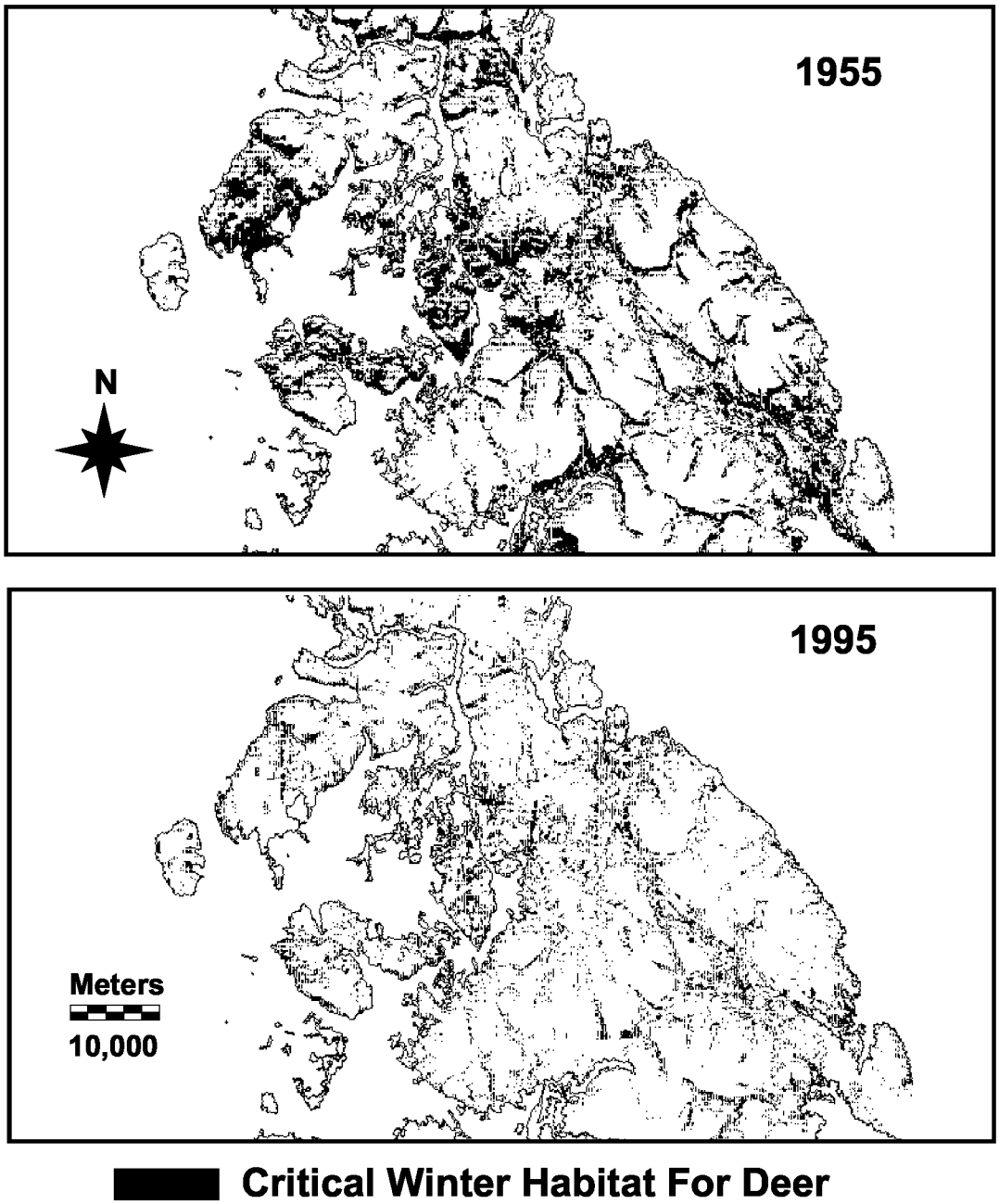

Figure 4. Critical winter habitat for Sitka black-tailed deer within the north-central portion of Prince of Wales Island and other adjacent islands, Southeast Alaska, USA. Critical winter habitat was defined as closed-canopy old-growth forest <250 m in elevation on south-facing slopes (Wallmo and Schoen 1980, Schoen et al. 1988). Upper map shows winter habitat for deer that existed prior to the initiation of industrial-scale logging in 1955. The lower map shows winter habitat for deer in 1995.

have difficulty hunting in that habitat because of slash and debris left behind from logging. Overall, seral forests support few deer and likely are unproductive hunting grounds for wolves.

Unspecified private lands are those areas in private ownership for which detailed data on habitat are not available. Most of those lands are owned by Alaska Native corporations, and 70-80% of forest habitat has been clearcut on these lands since the early 1980s (Alaska Department of Fish and Game *unpublished data*).

Roads varied from improved highways to temporary roads. Most roads were constructed for purposes of harvesting timber and were surfaced with gravel or coarse crushed stone. Some older roads were overgrown with alder and spruce, but most were clear of vegetation. The U.S. Forest Service closed some roads by removing culverts and bridges; however, that policy was sporadic and most roads were open for vehicular traffic. People using all-terrain vehicles and snowmachines frequently bypassed roadblocks on closed roads. In addition, we observed frequent use by people in motorized vehicles of roads on islands that were not connected to towns or villages. Deer-hunting parties often brought small all-terrain vehicles with them on boats and remote logging camps usually included a fleet of vehicles. Indeed, hunters often employ multiple means of transportation in pursuit of game in Alaska (Albert et al. 2001).

We did not make a distinction between open and closed roads. Few roads were plowed during winter and their use by people largely was curtailed during snowy periods. During snow-free periods, human activities along forest roads included,

hunting, fishing, trapping, hiking, camping, berry picking, firewood gathering, sightseeing, and logging.

In addition to habitat classifications, we included elevation, distance from roads, and distance from lakes and streams as habitat variables that potentially would be important to wolves. The U.S. Forest Service provided coverages from their geographic information system (GIS) for the Tongass National Forest showing data on habitats and timber harvests, and USGS digital-elevation models (DEM) were used to estimate elevation. All data layers were converted to data with grid-cell sizes of 20 m and analyzed with GIS program IDRISI (Clark Laboratories, Worcester, Mass.).

Determining habitat use.—We analyzed habitat selection by wolves using a method modified from Samuel and Kenow (1992). Rather than assigning a single point estimate to each wolf relocation, we selected 50 randomly subsampled points from the probability space formed by the 95% multivariate-normal confidence ellipse surrounding the estimated position of the animal. Therefore, each wolf relocation was represented by a multivariate normal cluster of 50 points (we did not inflate our sample size by a factor of 50; n = number of radio locations). The shape, orientation, and dispersion of clusters of subsampled points reflected size and shape of the confidence region surrounding the estimated location of each wolf. Sizes of confidence ellipses for relocations from ground-based telemetry were determined by quality of the radio signals, bearing errors, distances from the animals, and angles between successive bearings used for triangulation. The 95% confidence ellipse around each aerial location was circular, with a radius of 100 m.

Each cluster of subsampled points was plotted on our GIS background layers, and habitat type, distance from roads, distance from lakes and streams, and elevation were recorded for each point. Therefore, for each wolf relocation, we recorded frequency with which subsampled points overlaid each habitat type. Measures of elevation and distance were averaged over the 50 subsampled points. We estimated habitat available to each wolf pack by encompassing the home range of each pack by a rectangle (Pierce et al. 2000). Each rectangle was defined by the major north-south and east-west axes of the home range multiplied by 1.5. Thus, habitats within the home range and those immediately adjacent to it were included in our estimate of available habitat. Those additional areas outside the home ranges were necessary to assess habitat selection by wolves because habitat features outside the home ranges affect the distribution of animals across the landscape (Kie et al. *in press*). We matched each cluster of points representing a relocation for a resident wolf with an identically sized and distributed cluster of points with its centroid located randomly within the rectangle associated with the pack. We matched each cluster of points representing a relocation for a dispersing or extraterritorial wolf with an identically sized and distributed cluster of points with its centroid located randomly within boundaries of game management unit 2.

Statistical procedures.— We estimated median days of survival and estimated survival and hazard functions using the Kaplan-Meier product-limit method (Efron 1988, Pollock et al. 1989). Survival functions for residents and nonresidents (dispersers and extraterritorials) were compared with log-rank tests (Lee 1992). We used a simple

Mann-Whitney *U* test to relate mortality to habitat characteristics such as habitat type and density of roads within the home range of each wolf.

We used stepwise logistic regression (α to enter = 0.15 and α to remove = 0.30) to compare habitat type, elevation, and distance measures associated with locations used by wolves with matched random locations within the home range. We used Hosmer and Lemeshow goodness-of-fit statistics (Hosmer and Lemeshow 1989) and percent correct classification of jackknifed data series as criteria for selecting the best models. We carefully monitored changes in coefficients and their standard errors during the stepwise process to avoid the confounding effects of multicollinearity on the model outcomes (Hosmer and Lemeshow 1989). We considered coefficients as weakly important if their *P*-values were >0.1 and ≤0.15, important if their *P*-values were >0.05 and ≤0.1, and very important if their *P*-values were ≤0.05. The sign of the coefficient was interpreted as the direction of selection. Stepwise multiple regression (α to enter = 0.15 and α to remove = 0.30) was used to compare home-range size and pack size with habitat composition, and harvest rates of wolves with habitat composition and roads. Because regression variables that were not individually significant might interact with covariates to become significant (Dunn and Clark 1974), we relaxed *P*-values to include those potentially important variables. Effects of multicollinearity in regression models was reduced by screening for strong correlations ($r > 0.70$) among independent variables and using adjusted R^2 as a measure of model fit (Hosmer and Lemeshow 1989).

Fuller (1989) concluded that a 35% rate of mortality for wolves would result in population declines. Person et al. (1996) recommended a guideline that total mortality

should be ≤30–35% to reduce the risk of a wolf population decline on Prince of Wales and Kosciusko islands. Natural mortality may range between 5 and 10% in exploited populations (Fuller 1989); therefore, mortality from trapping and hunting should not exceed 25-30%. We chose the mid-point of this range (28%) to represent the limit of sustainable harvest, a value also suggested by Fuller (1989). We used stepwise logistic regression (α to enter = 0.15 and α to remove = 0.30) to assess habitat composition and roads as predictors of unsustainable wolf harvest. Mann-Whitney, Kruskal-Wallace, and Chi-square tests of independence were used when simple univariate and multivariate comparisons were made. We used program StatXact (Cytel Corp., Cambridge, Mass.) to calculate exact *P*-values for those tests.

Predator-prey Modeling

We constructed a relatively simple population model for wolves and deer on Prince of Wales and adjacent islands (game management unit 2) using a series of difference equations (Gilpin and Ayala 1973, Eberhardt 1998, Eberhardt and Peterson 1999, Person et al. 2001). We used the model to simulate populations of wolves and moose on Isle Royale, Michigan (Peterson and Page 1988), and wolves and deer on Coronation Island, Alaska (Klein 1995), to determine if predictions from the model were consistent with empirical data. We simulated the model 2,000 times using Monte Carlo techniques for both wolf-ungulate systems.

The insular predator-prey system on Isle Royale has received widespread attention and is well documented in the literature (Mech 1966, Jordan et al. 1967, Mech 1970, Peterson 1977, Allen 1979, Peterson and Page 1988, Peterson 1995). Therefore, Isle

Royale offers a good benchmark against which to test predictions from our model. The case history of wolves on Coronation Island is less well known. Coronation Island is 79 km^2 and is located in Southeast Alaska. Sitka black-tailed deer occur on the island, but wolves likely were historically absent (Klein 1995). In 1960, 2 adult male and 2 adult female wolves were introduced to the island. In 1961, both females were shot by a hunter and in 1963 another adult female wolf was introduced to the island. Four years after the original introduction the population reached a peak of 13 animals. The population of deer, which were probably at carrying capacity (K) when wolves were introduced, declined precipitously until numbers were so low that wolves consumed mostly alternative prey such as marine mammals and waterfowl (Klein 1995). By 1970, the population of wolves had disappeared and deer numbers increased rapidly.

After testing our model against empirical data from Isle Royale and Coronation Island, we used the model to predict effects of timber harvest and road construction on the wolf-deer system on Prince of Wales and nearby islands (Alaska Dept. of Fish and Game, game management unit 2). We divided game management unit 2 into distinct pack areas that were equivalent in size to the average home range of a wolf pack. Carrying capacity for deer (K) was estimated with the deer habitat capability index (HCI) associated with each pack area (U. S. Forest Service 1997). Current lengths of road and land-use patterns were tabulated for each area. Changes in roads, land use, and K were projected for 50 years to reflect road construction and plans for harvesting of timber described in the Tongass Land Management Plan (U. S. Forest Service 1997).

The predator-prey model was applied to each area, which were linked in the model by a function representing dispersal of wolves.

Finally, we conducted simulations of our model for a single wolf pack, with no avenue for dispersal or immigration, to predict the minimum *K* for deer required to sustain a pack for 50 years. We excluded effects of roads or wolf and deer harvest so that we could focus on quality of habitat. We conducted 2,000 simulations using Monte Carlo techniques and compared results with historical data concerning the continuous presence of wolves on islands in game management unit 2 since 1955. Few reliable data concerning the presence or absence of wolves before 1955 were available. Historical data were derived from interviews with Alaska Natives, trappers, hunters, fisherman, and biologists, and from data on wolf harvest (Alaska Department of Fish and Game 1999).

Model description.— The deer component of the model took the form:

$$U_{t+1(i)} = U_{t(i)} + R_{t(i)} - CP_{at(i)} - H_{t(i)}, \qquad (1)$$

where,

$U_{t(i)}$ = spring deer population prior to parturition in vicinity of wolf pack *i*,

$R_{t(i)}$ = recruitment in deer population in vicinity of wolf pack *i*,

$CP_{at(i)}$ = predation mortality in vicinity of wolf pack *i*, and

$H_{t(i)}$ = deer harvest in vicinity of wolf pack *i*.

The total deer population = $\boldsymbol{U_t} = \sum_{i=1}^{j} U_{t(i)}$, where j = number of wolf packs.

Recruitment in the deer population was modeled with a theta-logistic function (Gilpin and Ayala 1973, Eberhardt 1998, Eberhardt and Peterson 1999, Person et al. 2001):

$$R_{t(i)} = U_{t(i)}\, r_{\max}\left[1-\left(\frac{U_{t(i)}}{K_{t(i)}}\right)^{\theta}\right] \qquad (2)$$

where,

r_{max} = maximum per capita rate of increase in the absence of predation and hunting,

θ = density-dependence parameter,

$K_{t(i)}$ = carrying capacity for deer, defined as the number of deer that can be sustained through winter in the vicinity of wolf pack i; and

$R_{t(i)}$ = represents all recruitment and all compensatory mortality in the absence of predation and hunting.

Mortality from wolf predation was represented as:

$CP_{at(i)}$,

where,

C = deer killed per wolf per year, and

$P_{at(i)}$ = average number of wolves in pack i in year t = $(P_{t(i)}+(P_{t(i)}+ S_{t(i)}))/2$.

Mortality from predation and hunting in the model is additive (Gasaway et al. 1992, Hayes 1995), and predation rate is constant despite changes in deer density. Although some researchers have suggested that a type II functional response is appropriate for wolves preying on moose and caribou (Messier 1994, Dale et al. 1994), effects of

density-dependent predation rates are small unless the prey population is at very low density (Marshal and Boutin 1999, Person et al. 2001). No data concerning the shape of the functional response curve for wolves and deer have been published; therefore, we chose a constant predation rate to simplify the model.

Number of deer removed by hunting reflected effects of roads. We regressed average number of deer harvested by wildlife analysis area against length of roads within a particular wildlife analysis area. Separate regression models were derived for those areas connected to the main system of roads on Prince of Wales Island and for those wildlife analysis areas that were not connected. The annual mortality of deer from hunting was represented as:

$$H_{t(i)} = (U_t + R_{t(i)})h\,(1+\beta_d \times Km\ Roads) \quad \text{where,} \qquad (3)$$

h = base rate of harvest in the absence of roads, and

β_d = coefficient representing the additional harvest due to road access.

The wolf population was calculated by the following equation:

$$P_{t+1(i)} = P_{t(i)} + S_{t(i)} - T_{t(i)} - D_{t(i)} - M_{t(i)} + I_{t(i)} \qquad (4)$$

where,

$P_{t(i)}$ = Pack size in spring prior to parturition for wolf pack in area i,

$S_{t(i)}$ = reproduction in pack in area i,

$T_{t(i)}$ = wolves harvested from pack in area i,

$D_{t(i)}$ = dispersal from pack in area i,

$M_{t(i)}$ = natural mortality in pack in area i, and

$I_{t(i)}$ = immigration from other packs.

Human access by roads influences number of wolves killed by trapping or hunting. Similar to the deer model, we regressed average number of wolves harvested by wildlife analysis area against length of road within that area. Separate regression models were derived for those areas connected to the main system of roads on Prince of Wales Island and for those wildlife analysis areas that were not connected. The annual mortality of wolves in pack area *i* from hunting was represented as:

$$T_{t(i)} = (P_{t(i)} + R_{t(i)})q(1+\beta_w \times km\ roads) \qquad (5)$$

where,

q = base rate of harvest in the absence of roads, and

β_w = coefficient representing the additional harvest because of road access.

Rates of dispersal and nonhuman-related mortality in wolves have been linked to the availability of ungulate prey (Ballard et al. 1987, Peterson and Page 1988, Gese and Mech 1991). Effects of ungulate numbers on mortality and dispersal may be delayed, however, because of availability of other prey such as beaver, which may sustain wolves temporarily. Peterson and Page (1988) suggested that on Isle Royale, beaver may buffer effects of a decline in moose on mortality of wolves for 2–3 years. We represented dispersal ($D_{t(i)}$) and natural mortality ($M_{t(i)}$) in pack (i) by the following equations:

$$D_{t(i)} = \left(P_{t(i)} + S_{t(i)} - T_{t(i)}\right)\left[d\left(\frac{CP_{t(i)}}{\alpha\ U_{t-2(i)}}\right)\right], \qquad (6)$$

where,

d = dispersal rate when consumption of prey equals the number of prey available,

$CP_{t(i)}$ = number of deer consumed by wolf pack i, and

$\alpha U_{t\text{-}2(i)}$ = number of deer available at time *t-2* (2-year time lag).

$$M_{t(i)} = \left(P_{t(i)} + S_{t(i)} - T_{t(i)} - D_{t(i)}\right)\left[m\left(\frac{CP_{t(i)}}{\alpha\ U_{t\text{-}2(i)}}\right)\right] \qquad (7)$$

where,

m = mortality rate when consumption of prey equals number of prey available,

$CP_{t(i)}$ = number of deer consumed by wolf pack *i*, and

$\alpha U_{t\text{-}2(i)}$ = number of deer available at time *t-2* (2-year time lag).

Our model allowed pack areas that were unoccupied or occupied by a single wolf to accept immigrants. Vacant areas were colonized by pairs of wolves if wolves were available in the pool of dispersers (D_t), and areas with only 1 wolf could accept 1 additional animal from the pool of dispersers. No pack area could be colonized unless there were sufficient prey to support 1 pair of wolves. Acceptance of unrelated wolves into existing wolf packs has been well documented (Mech et al. 1998); nonetheless, dynamics involved are complicated and beyond the scope of our model. Further, addition of a single wolf to a pack is unlikely to alter dynamics between the pack and its prey sufficiently to warrant inclusion in our model. In contrast, recolonization of vacant pack areas is extremely important with respect to predator-prey dynamics. We represented immigration as:

$$I_{t(i)} = \text{immigration to area } i = \begin{cases} 1 \text{ or } 2, \text{if } P_{t(i)} < 2 \text{ and } D_t > 0, \text{and } \dfrac{CP_{t(i)}}{\alpha\, U_t} > 2 \\ 0, \text{otherwise}. \end{cases} \qquad (8)$$

Total number of dispersers in the population was calculated by:

$$D_t = \text{total dispersers in population} = s_d \sum_{i=1}^{j} D_{t(i)} - \sum_{i=1}^{j} I_{t(i)} \quad (9)$$

where,

s_d = annual survivorship for dispersers.

$$\text{The total wolf population} = P_t = D_t + \sum_{i=1}^{j} P_{t(i)} \quad (10)$$

where,

j = number of pack areas.

The model does not consider sex and age structure of the deer population directly, however, changes in sex and structure are implicit in the function for recruitment as the population approaches K (Bowyer et al. 1999). All sex and age classes are assumed to be equally vulnerable to predation and the sex ratio of the deer population was set at 1:1. Age structure and sex ratios probably influence predator-prey interactions between wolves and deer (Mech 1970, Kolenosky 1972, Fuller 1989). Inclusion, however, of age- and sex-specific rates of predation in early versions of the model did not produce outcomes that were different from versions that excluded those factors. Therefore, we ignored age structure and sex ratios of deer populations to simplify our model. Spatial segregation of the sexes of deer outside the mating season (Bowyer 1984, Bowyer et al. 1996, Kie and Bowyer 1999, Barboza and Bowyer 2000) holds the potential to affect wolf-deer interactions, but empirical data to evaluate that pattern are lacking. Likewise, risk of predation may affect the distribution and behavior of ungulates (Berger 1991, Molvar and Bowyer 1994, Rachlow and Bowyer 1998, Kie 1999). Unfortunately, we

lack empirical data to parameterize our wolf-deer model for those potentialities. We assumed that deer are removed first by wolf predation, and hunting was allocated what remained. Wolves prey on deer year-round and kill both sexes. Legal hunting occurs for 5 months beginning in August and primarily removes adult males from the deer population. Further, the legal bag limit for a hunter is 4 deer/year. Hunters harvest from 2,000 to 3,000 deer per year from game management unit 2, whereas, wolves probably remove from 6,000 to 11,900 deer of either sex annually. Clearly, predation by wolves will have a much greater effect on deer than current levels of hunting, and is therefore given priority in the model. Nonetheless, deer are killed by wolves and humans simultaneously during the hunting season, and when deer populations are very low, wolves realistically may not have priority. Consequently, our model presents an optimistic scenario for wolves when deer populations are low.

Population dynamics of wolves within the model are primarily a function of the availability of ungulate biomass (Keith 1983, Fuller 1989, Gasaway et al. 1992, Person et al. 2001). The model assumes that natural rates of mortality and dispersal are compensatory with mortality from trapping or hunting (Ballard et al. 1987, Fuller 1989).

We assumed that wolf and deer populations on Prince of Wales and adjacent islands are closed with an insignificant probability of dispersal to and from the area. In 2000, a female wolf that was radiocollared as part of another study crossed Prince of Wales Island and swam across Clarence Strait to the mainland (Alaska Department of Fish and Game *unpublished data*). Nevertheless, that female is the only 1 of 45 wolves radiocollared on Prince of Wales and the adjacent islands since 1992 to disperse from

game management unit 2. Such limited dispersal to and from that game management unit probably has little influence on population dynamics of wolves.

Simulating winters.—Based on data for temperature and precipitation from the National Weather Service on Annette Island and Sitka (National Weather Service 1998), and data from Alaska Department of Fish and Game (*unpublished data*), approximately 6 winters per century may result in general declines in deer numbers in the southern portion of the Alexander Archipelago. Those events seem to follow a random-walk model (autocorrelation $\rho < 0.13$, $P > 0.05$), and can be simulated by assuming a probability of 0.17 that any particular year will include a severe winter:

$$\Pr(x = 6) = \frac{100!}{94!6!}\left(\frac{6}{100}\right)^{6}\left(1 - \frac{6}{100}\right)^{94} = 0.166 \text{ or } \approx 0.17 .$$

In our simulations, a severe winter resulted in a complete loss of recruitment. In reality, severe winters may result in the loss of both juveniles and adults. For example, in a telemetry study of deer in the northern portion of the Alexander Archipelago, where wolves do not occur, 60% of radio collared adult deer died during 1 severe winter (Kirchhoff *pers. comm.*). Nonetheless, Klein (1965*b*) reported that winter mortalities from malnutrition were lower in areas where deer were exposed to predation by wolves. Where predation occurs, deer are probably below *K*, and more likely to survive a severe winter. Therefore, we selected a relatively optimistic scenario; severe winters of 1969-1970 were included in each simulation, and severe winters occurred randomly after 1995.

Boot-strapped Monte Carlo techniques were used in simulations of the model (Hilborn and Mangel 1997). The probability distributions for each parameter encompassed process variation within biologically appropriate ranges. In addition, probability distributions also accounted for sampling variances associated with estimates of those parameters.

RESULTS

Ecology of wolves in Southeast Alaska

Home range.—We obtained 1,488 radio relocations of 23 wolves from 7 packs. One-half (49.9%) of those radio relocations were obtained during the denning season (15 April – 1 August). Home ranges were estimated for 12 resident and 3 extraterritorial wolves that had >30 relocations (Table 1). Minimum convex polygon (MCP) and 95% adaptive kernel (ADK) home ranges for resident wolves were about 7 times larger than the 50% ADK home ranges (core areas). Composite MCP and 95% ADK home ranges for wolf packs (Fig. 5) were larger than those of individual wolves, but core areas were similar in size (Table 1).

Home ranges were much smaller during pup-rearing season, with core areas about one-half the size of autumn and winter core areas (Table 1). The presence of young pups likely was the cause of those differences. For example, in 1994 the Kosciusko Island and Kasaan Peninsula packs did not reproduce successfully. Although number of radio locations for each pack during pup-rearing season was <30 in any particular year, sample sizes were equivalent between seasons and packs. Therefore, a comparison of home ranges by year for each pack was possible. In 1994, MCP home ranges for the

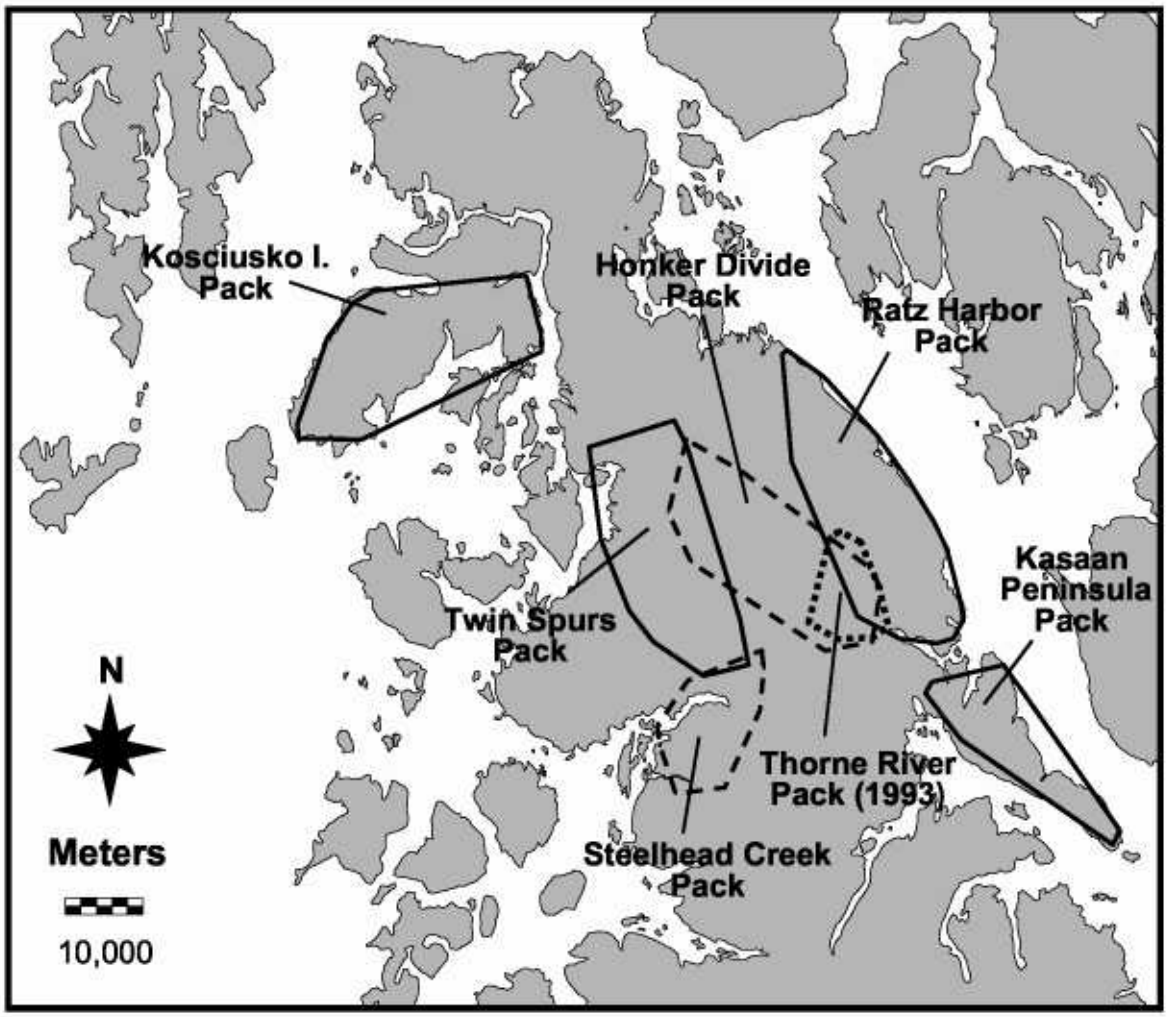

Figure 5. Study area showing Mohr's convex polygon home ranges for 7 wolf packs on Prince of Wales and Kosciusko islands, Southeast Alaska, USA. The Thorne River pack disappeared after 1993 and the Honker Divide pack absorbed that home range in 1994.

Table 1. Means for Mohr's convex polygon (MCP), 95% adaptive kernel (ADK95), and 50% adaptive kernel home ranges (ADK50) for individual resident wolves, wolf packs for which all seasons are combined, wolf packs during pup-rearing season, and extra-territorial wolves. Wolves were monitored between March 1993 and October 1996 on Prince of Wales and Kosciusko islands in Southeast Alaska, USA.

	Home-Range Size (km^2)						
Category	MCP	SE	ADK95	SE	ADK50	SE	*n*
Residents	231.0	23.9	261.8	25.7	37.2	4.3	11
Packs (all seasons)	259.7	47.5	279.1	39.4	37.9	4.6	7
Packs (pup-rearing)	104.7	16.7	142.4	23.6	17.0	3.1	11
Extra-territorials	500.9	139.0	446.3	91.2	43.7	13.5	3

Kosciusko and Kasaan packs during pup-rearing season were 210.5 and 148.9 km^2, respectively. In contrast, both packs produced litters in 1995 and MCP home ranges were 52.6 and 85.5 km^2, respectively. Core areas for the Kosciusko Island pack were 72.9 km^2 in 1994, and 34.4 km^2 in 1995. The Kasaan Peninsula pack showed a similar pattern with their core areas encompassing 29.2 km^2 in 1994, and 8.8 km^2 in 1995.

Pack size and composition changed over time, with individuals or small groups of wolves occasionally splitting from the main pack, only to rejoin it days or weeks later. Indeed, all members of a wolf pack rarely were observed together, except during winter. Pack sizes could be estimated only after repeated direct observations. Number of wolves in a pack ranged from 2 to 13 (Table 2); nonetheless, observations of other wolf packs made by pilots and trappers suggested that some packs outside of the study area may have numbered ≥15 wolves.

Home range was strongly correlated with pack size. Because the constant in the regression of pack versus home range size was not significantly different from zero ($P > 0.05$), we repeated the analysis and forced the model through the origin (Fig. 6).

Extraterritorial and dispersing wolves.— Most (60%) of our 23 radiocollared wolves dispersed or exhibited extraterritorial behavior. Monthly number of radiocollared wolves that were nonresidents (dispersing and extraterritorial wolves) averaged 3.9 (SE = 1.7) between 1 May 1993 and 30 April 1994, and 2.8 (SE = 1.3) between 1 May 1994 and 30 April 1995. Annually, about 29% (SE = 12%) of our 23 radiocollared wolves were nonresidents.

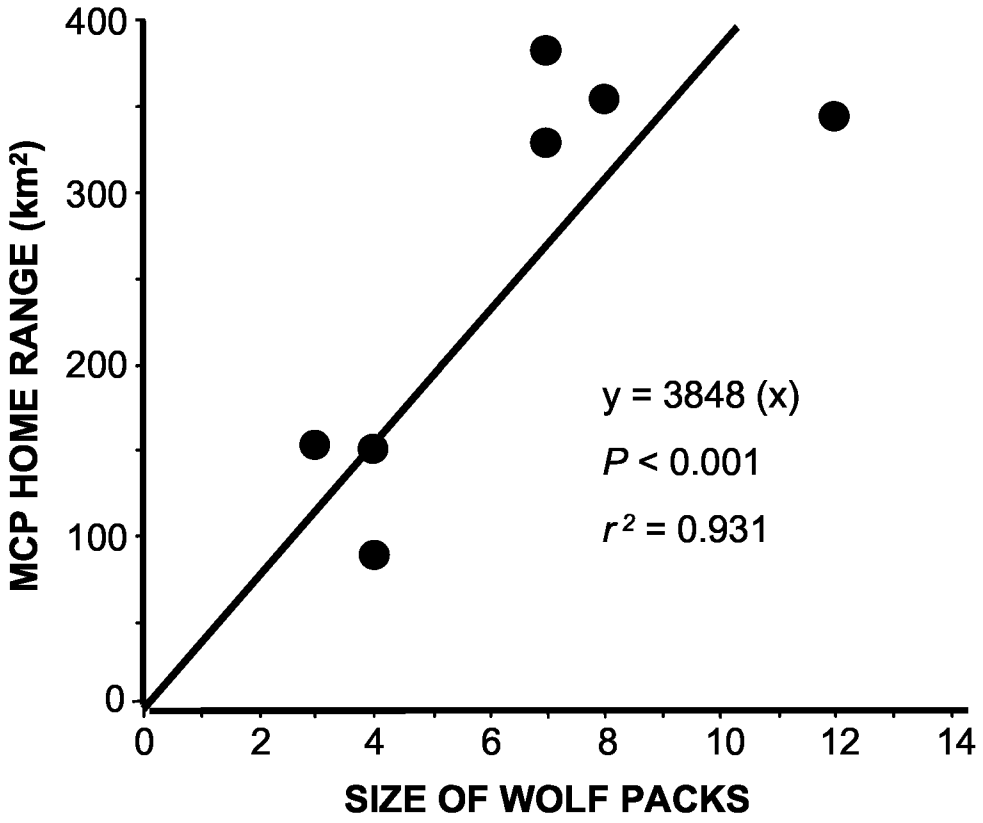

Figure 6. Regression of Mohr's convex polygon (MCP) home-range sizes for 7 wolf packs versus size of packs in autumn. Wolf packs were located on Prince of Wales and Kosciusko islands, Southeast Alaska, USA.

Table 2. Sizes of packs during autumn (Sept.–Nov.) for wolves on Prince of Wales and Kosciusko islands in Southeast Alaska, USA, 1993–95.

	Pack Size[a]		
Pack	1993	1994	1995
Ratz Harbor	8	7	6
Twin Spurs	11	8	8
Honker Divide	11	12	11
Kosciusko Island	9	4	8
Kasaan Peninsula	-	2	5
Steelhead Creek	-	0	3
Thorne River	4	0	0
Sunny Hay Creek[b]	-	13	-
Nossuk Bay[b]	-	8	-
Mean	8.6	7.7	6.8
SE	1.2	1.5	1.1

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[a] Dashes indicate that no data were available.

[b] Packs did not contain radiocollared wolves.

Fifteen radiocollared wolves were monitored as resident pack members. Of those animals, 8 dispersed and 4 settled and established new home ranges. Three wolves originally were captured as dispersers, 1 of which appeared to settle and establish a home range. Thus, 11 wolves exhibited dispersal behavior.

Seven of 8 resident wolves that dispersed left their home ranges between February and June. Six dispersing wolves were adults, 2 were yearlings, and 3 were juveniles. Two adults and both yearling dispersers were females. Minimum dispersal distances ranged between 7.2 and 255.5 km; median dispersal distance was 63.1 km (interquartile range = 178.2 km; Fig. 7). No dispersing wolves left Prince of Wales or the adjacent islands; however, some wolves must have swam at least 2 km in the open ocean to reach their final destinations. Five dispersing wolves settled and established home ranges. Two of those animals died within 2 months of settling and a third died within 8 months. All of those wolves apparently were alone. The other 2 wolves, which were both females, paired with males and successfully produced litters. Nonetheless, 1 female was killed by a hunter after occupying a home range for 7 months, and the other survived in its new home range for 18 months before being shot illegally.

One adult male, 1 adult female, and 1 yearling female exhibited extraterritorial behavior by maintaining a loose affiliation with a resident pack, but spending most of their time outside the home range of that pack. Home ranges for extraterritorial wolves were very large (>340 km^2) compared with those of resident wolves (Fig. 8, Table 1). The adult female settled in an area adjacent to the home range of the resident pack associated with her during summer 1993. Wolves were trapped and hunted intensively

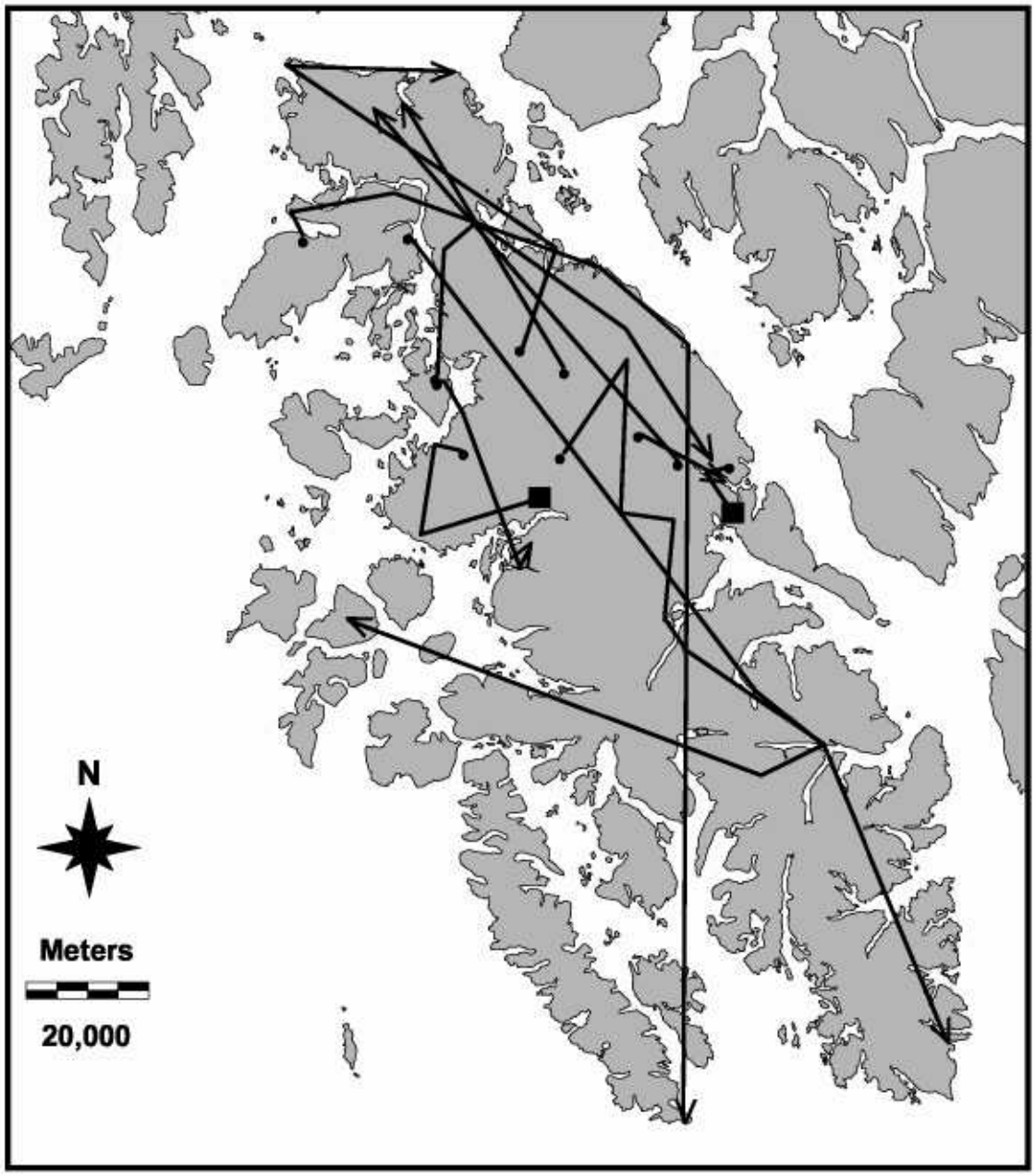

Figure 7. Minimum lengths of routes traveled by 11 dispersing wolves on Prince of Wales and adjacent islands, Southeast Alaska, USA. Arrowheads indicate locations where wolves were killed and squares indicate locations where wolves settled.

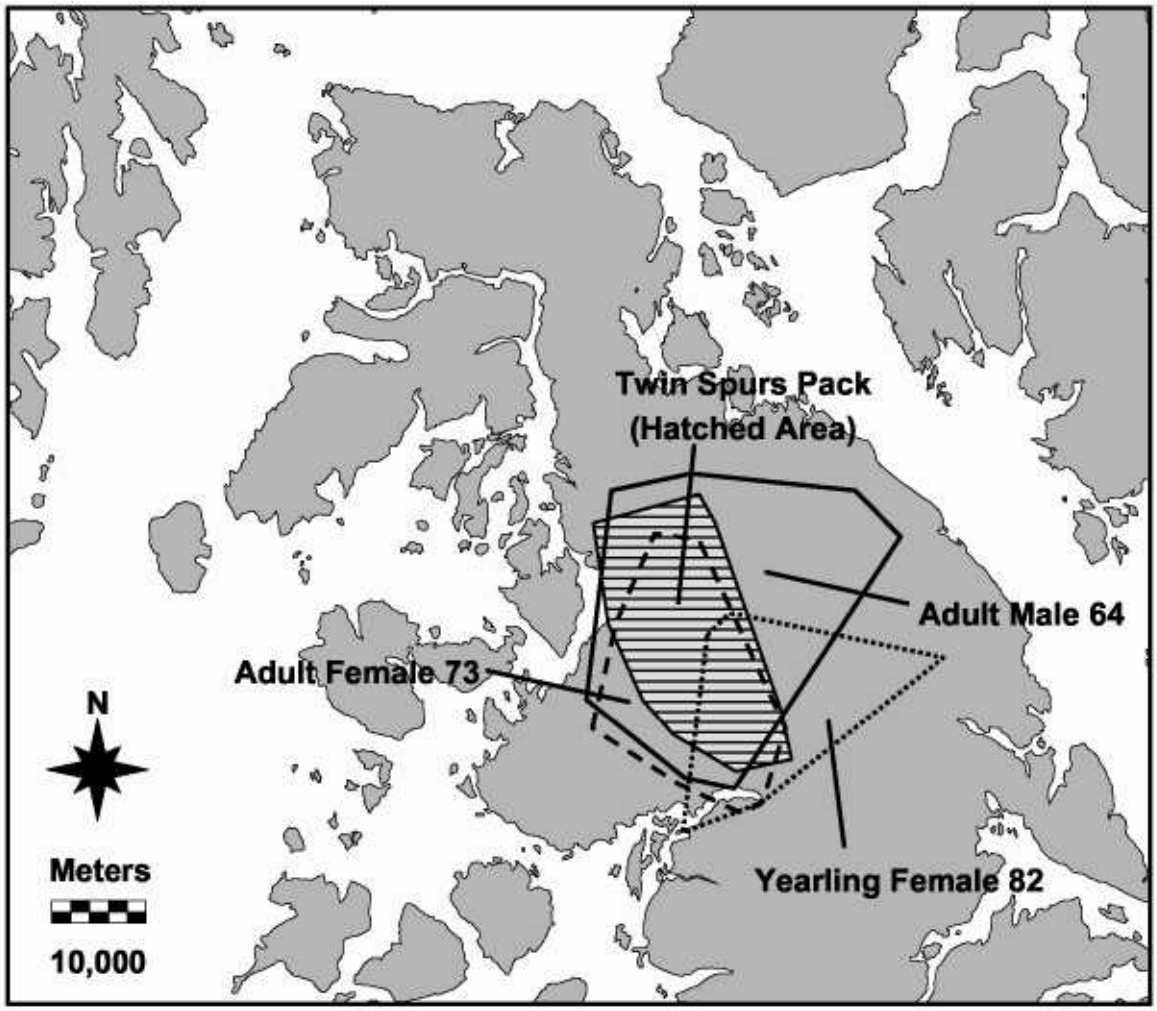

Figure 8. Study area showing the Mohr's convex polygon home ranges for 3 extraterritorial wolves on Prince of Wales Island, Southeast Alaska, USA. Hatched area indicates the home range of the Twin Spurs pack, with which extraterritorial wolves likely were associated.

in this particular area in 1992 and 1993, and the resident pack may have been exterminated. The adult female likely was alone when she was trapped in December 1993. The yearling female settled in that same area during spring 1994. Tracks indicated that she was accompanied by another wolf, probably a male (owing to the large size of the tracks). She died of wounds from a fight with a black bear in spring 1994 before we could determine her reproductive status. The adult male that exhibited extraterritorial behavior continuously orbited the Twin Spurs pack from October 1993, until he was shot illegally in February 1995.

Opportunities for dispersing and extraterritorial wolves to settle may have been influenced by wolf harvest. Two female wolves dispersed into areas immediately adjacent to their original home ranges. In both instances, wolves had been harvested heavily in the adjacent areas and may have been exterminated. Five other dispersing or extraterritorial wolves settled in areas where wolves had been intensively trapped and hunted. In a 1,300 km^2 area on the north end of game management unit 2, a single trapper killed 42 wolves during winter 1992–93. The following year, 2 radiocollared wolves from north-central Prince of Wales Island dispersed and attempted to settle in that area. Within 7 months of settling, 1 was trapped legally and the other was shot illegally.

Mortality.— In game management unit 2, 851 wolves were reported killed by hunters and trappers from 1990 to 1998 (Alaska Department of Fish and Game 1999, Table 3). About 60% of mortality was from trapping (including snaring) and 40% from hunting (i.e., ground shooting). The highest proportion (21%) of mortality reported by

Table 3. Wolf harvest by year and category of transport to hunting and trapping areas for Prince of Wales and adjacent islands (GMU 2) in Southeast Alaska, USA, 1990–98.

	Year									
Type of Transport	90	91	92	93	94	95	96	97	98	Total
Airplane	2	2	1	1	1	3	0	0	1	11
Boat	15	53	68	59	58	56	47	51	45	452
Road Access	46	31	36	42	26	39	85	29	44	378
Unknown	3	0	0	1	0	5	0	0	1	10
Total Harvest	66	86	105	103	85	103	132	80	91	851

hunters and trappers occurred in December and January during the peak of the trapping season.

Seventeen of 23 wolves, which were successfully radiocollared and released, died during the course of our study. Seven of those were killed legally by hunters or trappers, and 7 were killed illegally by people. The unreported mortality from hunting or trapping that we observed indicated that the reported harvest of wolves during hunting and trapping seasons may underestimate human-caused mortality by as much as 50%.

Three wolves died of causes unrelated to human activity. One of those appeared to have died of wounds from an encounter with a black bear, and the cause of death for the others could not be determined. All wolves that died from natural causes were extraterritorials or dispersers. No resident wolves died from causes other than hunting or trapping. Clearly, humans were the overwhelming cause of wolf mortality during the 3 years of our study.

Annual survivorship between 1 November 1993 and 31 October 1994 was 43% (SE = 15%) and between 1 November 1994 and 31 October 1995 was 46% (SE = 20%) (Table A-1). Overall, survivorship for those 2 years was 20% (SE = 16%). Our sample size was too small to rigorously compare age- and sex-specific survivorship. Two of 6 wolves monitored as pups, 4 of 8 wolves monitored as yearlings, and 11 of 14 wolves monitored as adults, died. Mortality rate was 73% (8/11) for males and 75% (9/12) for females. Log-linear analysis of death by age, sex, and resident status (resident versus

APPENDIX

Table A-1. Monthly survival rates (*s*) , survivorship (*l*), and causes of death for 23 radio-collared wolves on Prince of Wales and Kosciusko Islands, Southeast Alaska.

Month	Alive	Died	*s*	*l*	Cause
Nov 93	17	0	1	1	
Dec 93	16	4	0.75	0.75	4 wolves trapped
Jan 94	12	1	0.92	0.69	1 wolf trapped
Feb 94	13	0	1	0.69	
Mar 94	13	1	0.92	0.63	1 wolf trapped
Apr 94	12	3	0.75	0.48	2 wolves trapped, 1 wolf killed by bear
May 94	9	0	1	0.48	
Jun 94	9	0	1	0.48	
Jul 94	10	0	1	0.48	
Aug 94	10	1	0.90	0.43	1 wolf shot
Sep 94	10	0	1	0.43	
Oct 94	10	0	1	0.43	
Nov 94	13	0	1	0.43	
Dec 94	13	1	0.92	0.40	1 wolf died of natural causes
Jan 95	12	0	1	0.40	
Feb 95	12	3	0.75	0.30	2 wolves shot, 1 wolf died of natural causes
Mar 95	9	0	1	0.30	
Apr 95	9	0	1	0.30	
May 95	9	0	1	0.30	
Jun 95	9	0	1	0.30	
Jul 95	9	1	0.89	0.26	1 wolf shot
Aug 95	8	1	0.88	0.23	1 wolf shot
Sep 95	7	1	0.86	0.20	1 wolf shot
Oct 95	6	0	1	0.20	

extraterritorial or disperser) indicated that only resident status was related to probability of death (partial $\chi^2_4 = 5.16$, $P = 0.023$).

Dispersers and extraterritorial wolves had higher mortality than resident pack members (79% versus 39%; Fishers exact test = 5.670, $P = 0.029$). Annual rate of mortality was 64% (SE = 14%) for nonresidents and 31% for residents. Shape of the survival function for resident wolves was different than that for nonresidents (Log rank test $\chi^2_1 = 5.3$, $P = 0.021$; Fig. 9). Median duration of radio tracking before death for nonresident wolves was 24 weeks, whereas for residents it was 90 weeks. The hazard function (instantaneous rate of death) for resident wolves was best approximated by an asymptotic function (Fig. 9). In contrast, the hazard function for nonresidents was a linear function (Fig. 9), and therefore increased at a constant rate. That difference occurred because mortality in resident wolves was the result of hunting and trapping, which was seasonal. Consequently, the cumulative hazard rate increased rapidly during the hunting and trapping seasons and then leveled off between seasons (Fig. 9). Nonresidents were subject to seasonal mortality from hunting and trapping and natural mortality, for which no seasonal pattern was observed. The longer a wolf remained as a nonresident, the higher its probability of death (Fig. 9). Hazard functions predicted that a hazard rate at which one-half the wolves alive at time t would die during the next 2 weeks would be reached after 12 weeks for nonresidents, and 35 weeks for residents. The odds ratio for death by resident status indicated that nonresident wolves were 6.7 times more likely to die compared with resident wolves. Clearly, dispersal and extraterritoriality were risky behaviors.

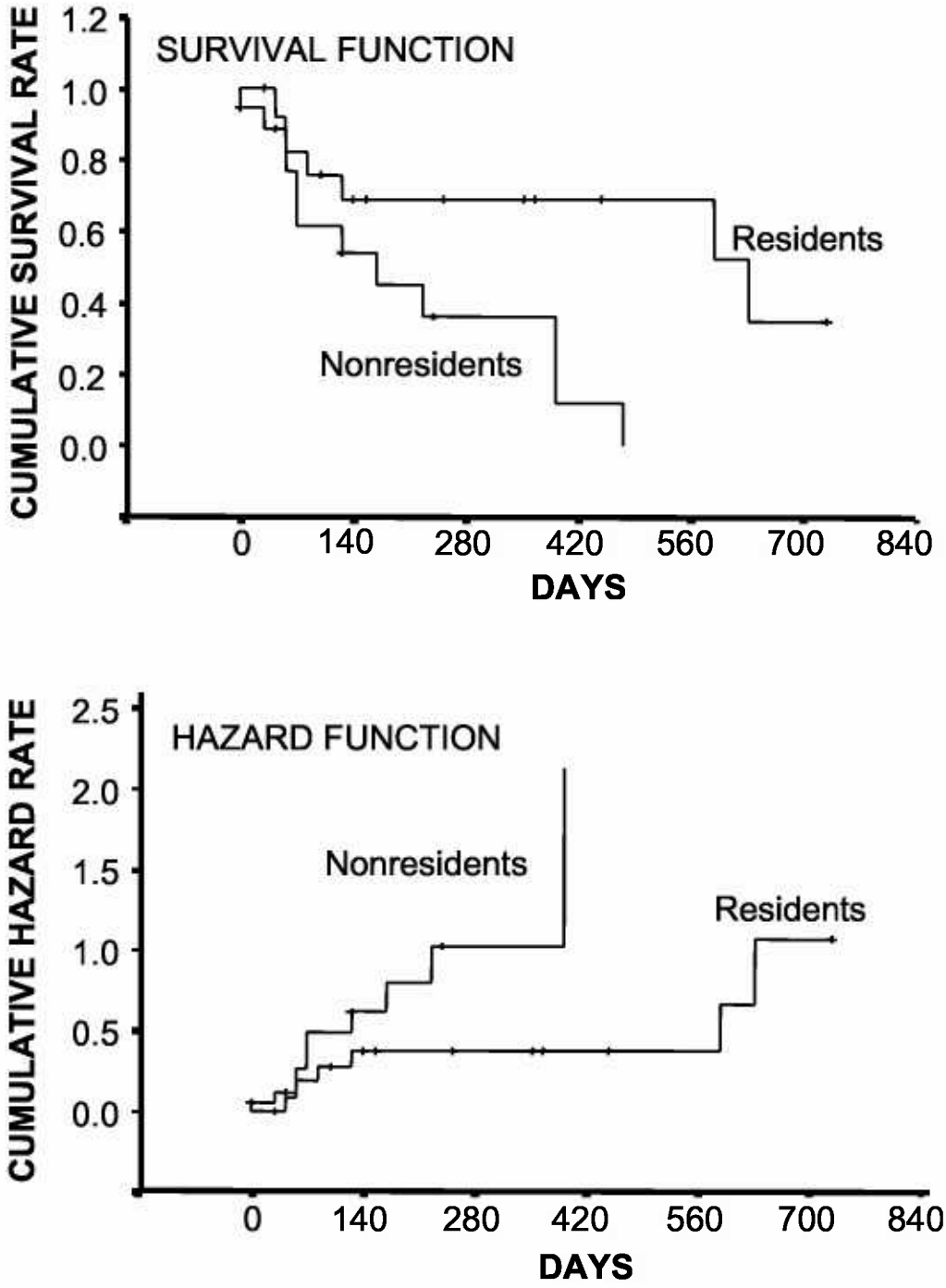

Figure 9. Survival and hazard functions for 15 radiocollared wolves monitored as residents and 14 radiocollared wolves monitored as nonresidents on Prince of Wales and adjacent islands, Southeast Alaska, USA. Monitoring took place between March 1993 and September 1995.

Reproduction and denning— Wolves used dens from mid-April to early July. Activity peaked around den sites from early May to the third week in June. From mid-June to mid-August, activity concentrated near rendezvous sites, which were areas where pups remained while adults foraged. Of 22 den sites examined between October 1992 and October 1999, all were in old-growth forest within 100 m of fresh water. One den was under a large log; all others were in cavities beneath the roots of large trees (>80 cm dbh). Ten of 18 active dens visited were adjacent to ponds or streams with colonies of beavers.

We saw no evidence of multiple pairs breeding among the 7 packs that we monitored on Prince of Wales and Kosciusko islands. Pups observed at dens in late May and early June were about 4-5 weeks old, indicating that parturition occurred during the last 2 weeks of April. Assuming a gestation period of 63 days, mating probably took place in late February or early March.

We were able to count pups at 6 dens in early June 1995. Number of pups ranged from 1 to 6 ($\bar{x}$ = 3.7, SE = 1.8). Three radiocollared females were first-time breeders and produced 1, 3, and 4 pups, respectively. Three other wolf packs produced 3, 5, and 6 pups. In addition, a wolf pack on Heceta Island observed during June 1997–99 had 4, 4, and 5 pups ($\bar{x}$ = 4.3, SE = 0.6), respectively (C. Farmer *pers. comm.*). Further, an average of 4.3 pups (SE = 1.4, Range = 2–6) were observed at 7 dens on Prince of Wales Island visited in spring 2000–01 as part of an ongoing wolf research project (Alaska Department of Fish and Game *unpublished data*). Thus, 4 is likely the average number of pups per pack in early summer. Direct observations made during early autumn 1995

revealed that only 1 pup from the total number seen at the dens had disappeared, suggesting high survivorship of pups during summer.

Habitat analysis.—We compared habitat used by pack members during different biological seasons versus random locations within and in the vicinity of their pack home ranges. Wolves spent most of their time at low elevations regardless of biological season (Tables 4 and 6). Indeed, 50% of 920 radio-locations for resident wolves were <82 m and 95% were <396 m in elevation. Seasonal differences were pronounced in 4 packs with mean elevation for 3 packs lower during the pup-rearing season than at other times of the year. The exception was the Steelhead Creek pack, which denned at a much higher elevation (340 m) than other wolves. Tracks and radio locations indicated that most wolf packs occasionally traveled along ridge tops, even in deep snow during winter, but spent most of their time in valleys (Fig. 10).

Logistic-regression analysis, comparing radio locations with matched random locations, indicated that wolves selected for both open-canopy and closed-canopy old-growth forest at low elevation during the pup-rearing season (Tables 4 and 5, Table A-2). Avoidance of seral forest or clearcuts was exhibited by 3 packs during pup-rearing, but no similar patterns were discerned for the other 4 packs. Dens and rendezvous sites generally were located near fresh water and at low elevation. Dens usually were located in large patches of old-growth forest or muskeg at <250 m in elevation. Consistent with selection of den and rendezvous sites, distances from lakes and streams were less for radio locations of 3 packs than for matched random locations.

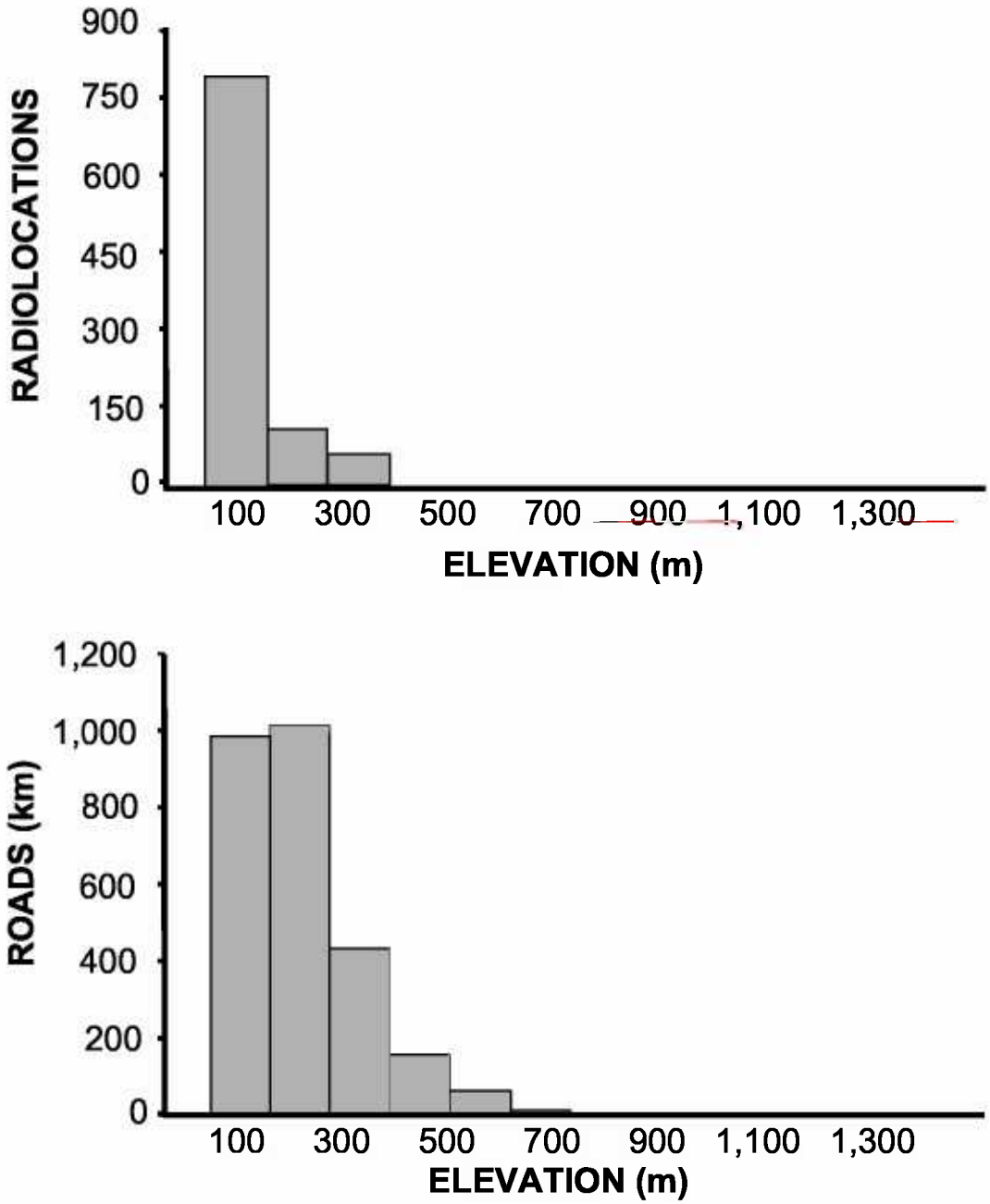

Figure 10. Number of radio locations for wolves and length of roads at different elevations within study area on Prince of Wales and Kosciusko islands, Southeast Alaska, USA.

Table 4. Simplified ranking matrix of elevation and distance measures for wolf packs during the pup-rearing period (15 April – 15 August) on Prince of Wales and Kosciusko islands in Southeast Alaska, USA. Matrix is based on the results from logistic regression of radio locations compared with random locations. Signs indicate direction of selection and number of signs indicates significance of selection (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$). Scores for each category are derived by adding positive signs and multiplying by number of packs with positive signs, and then subtracting the sum of negative signs multiplied by number of packs with negative signs. Scores provide a qualitative comparison of direction and strength of habitat selection.

	Elevation and Distance Measures		
Pack	Elevation[a]	Dist. from Road[a]	Dist. from Lake or Stream[a]
Ratz Harbor	– – –	– – –	
Twin Spurs	– – –	– – –	
Honker Divide	– –		– – –
Kosciusko I.	– – –	– – –	–
Kasaan Penin.			– – –
Steelhead Crk.			
Thorne River	– – –	– – –	+ + +

Score	-75	-48	-18

[a] Negative signs indicate that radio locations were at lower elevation or closer to roads, lakes, and streams than matched random locations.

Table 5. Simplified habitat ranking matrix for wolf packs during the pup-rearing period (15 April – 15 August) on Prince of Wales and Kosciusko islands in Southeast Alaska, USA. Matrix is based on results from logistic regression of radio locations compared with random locations. Signs indicate direction of selection and number of signs indicates significance of selection (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$). Scores for each category are derived by adding positive signs and multiplying by number of packs with positive signs, and then subtracting the sum of negative signs multiplied by number of packs with negative signs. Scores provide a qualitative comparison of direction and strength of habitat selection.

	Habitat Type[a]						
Pack	Lks	Ocog	Ccog	Seral	Ccut	Priv	Road
Ratz Harbor			+ + +		– – –		
Twin Spurs		+ + +					– – –
Honker Divide							
Kosciusko I.		+ + +	+ + +				
Kasaan Penin.				– – –			
Steelhead Crk.		+ + +			– –		+ +
Thorne River							

Score	0	+27	+12	-3	-10	0	-1

[a] Alpine habitat is excluded from analysis because it is strongly correlated with elevation. Codes for habitat types are as follows: Lks = lakes and streams, Ocog = open-canopy

old-growth forest and muskeg, Ccog = closed-canopy old-growth forest, Seral = second growth forest >25 years old, Ccut = second growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), and Road = road.

Table 6. Simplified ranking matrix of elevation and distance measures for wolf packs based on radio locations obtained before or after the pup-rearing period on Prince of Wales and Kosciusko islands in Southeast Alaska, USA. Matrix is based on results from logistic regression of radio locations compared with random locations. Signs indicate direction of selection and number of signs indicates significance of selection (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$). Scores for each category are derived by adding positive signs and multiplying by number of packs with positive signs, and then subtracting the sum of negative signs multiplied by number of packs with negative signs. Scores provide a qualitative comparison of direction and strength of habitat selection.

	Elevation and Distance Measures		
Pack	Elevation[a]	Dist. from Road[a]	Dist. from Lake or Stream[a]
Ratz Harbor	– – –	– –	
Twin Spurs	– – –	–	
Honker Divide	– – –	–	
Kosciusko I.		– – –	
Kasaan Penin.			– – –
Steelhead Crk.		–	
Thorne River	– – –	– –	+ + +

Scores	-48	-60	0

[a] Negative signs indicate that radio locations were at lower elevation or closer to roads, lakes, and streams than matched random locations.

Table A-2. Results for stepwise logistic regression of habitat type, elevation, and distance measures for wolf packs on Prince of Wales and Kosciusko Islands, Southeast Alaska during pup-rearing season. Results represent a comparison between radio locations of wolves (use) with matched random locations (available). Dashes indicate that the variable did not enter the model ($P > 0.15$).

Coefficients of Variables[a]

Wolf Pack	Elev.	Dist. Road	Dist. Lks	Lks	Ocog	Hvol	Seral	CCut	Priv	Road
Ratz Harbor	-0.004	-0.002	–	–	–	0.010	–	-0.018	–	–
Twin Spurs	-0.007	-0.001	–	–	0.018	–	–	–	–	-0.017
Honker Divide	-0.005	–	-0.004	–	–	–	–	–	–	–
Kosciusko Island	-0.007	-0.001	-0.001	–	0.013	0.013	–	–	–	–
Kasaan Peninsula	–	–	-0.003	–	–	–	-0.032	–	–	–
Steelhead Creek	–	–	–	–	0.020	–	–	-0.018	–	0.019
Thorne River	-0.039	-0.001	0.007	–	–	–	–	–	–	–

P-values of Coefficients

Wolf Pack	Elev.	Dist. Road	Dist. Lks	Lks	Ocog	Ccog	Seral	CCut	Priv	Road
Ratz Harbor	0.000	0.000	–	–	–	0.001	–	0.000	–	–
Twin Spurs	0.000	0.023	–	–	0.000	–	–	–	–	0.008
Honker Divide	0.064	–	0.009	–	–	–	–	–	–	–
Kosciusko Island	0.004	0.017	0.150	–	0.017	0.006	–	–	–	–
Kasaan Peninsula	–	–	0.002	–	–	–	0.017	–	–	–
Steelhead Creek	–	–	–	–	0.009	–	–	0.081	–	0.099
Thorne River	0.000	0.007	0.007	–	–	–	–	–	–	–

Regression Diagnostics

Wolf Pack	*n*	Hosmer-Lemeshow Goodness-of-Fit	*P*	% Correct Classification
Ratz Harbor	142	6.68	0.571	75.8
Twin Spurs	120	12.45	0.132	76.7
Honker Divide	48	6.93	0.544	69.5
Kosciusko Island	66	13.76	0.088	75.0
Kasaan Peninsula	34	4.76	0.783	70.6
Steelhead Creek	33	0.61	0.895	68.2
Thorne River	29	4.75	0.784	86.7

a. Codes for variables are as follows: Elev. = elevation in meters, Dist. Road = distance from nearest road in meters, Dist. Lks = distance from nearest lake or stream in meters, Lks = lake or stream, Ocog = open-canopy old-growth forest or muskeg, Ccog = closed-canopy old-growth forest, Seral = second-growth forest >25 years old, Ccut = second-growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), Road = temporary and permanent road. Alpine habitat was excluded because it was strongly correlated with elevation.

Nonetheless, 3 packs showed no significant affinity to lakes and streams, and 1 pack avoided streams and lakes (Table 5, Table A-2).

Patterns of habitat selection during the period before and after pup-rearing were less clear (Tables 6 and 7, Table A-3). Evidence existed for selection of closed-canopy old-growth forest, lakes and streams, and avoidance of seral forests and clearcuts (Table 7, Table A-3). The Ratz Harbor and Kosciusko Island packs selected for lakes and streams. Both of those packs frequently were located near the mouths of salmon-producing streams in late August and September. Indeed, the Kosciusko Island pack spent >1 month in late summer 1993 in the vicinity of an estuary on the southeastern corner of Kosciusko Island.

We expected to detect strong selection for closed-canopy old-growth forest by wolves because of its importance to deer in winter. The winters of 1993-94 and 1994-95 were mild; snow only accumulated after 15 November and remained until about 15 March. Therefore, we refined our analysis by examining only those locations obtained between November and April (Tables 8 and 9, Table A-4). Four packs had sufficient numbers of radio locations during that period to produce valid logistic-regression functions. Ratz Harbor and Honker Divide packs selected closed-canopy old-growth forest and the Kosciusko and Honker Divide packs showed weak affinity for open-canopy old growth. No other patterns of habitat selection were discerned. We did not detect patterns of habitat selection for the Twin Spurs pack during winter. That pack was located on the west coast of Prince of Wales Island, which is an area where snow depths rarely exceeded 20 cm during our study. Similarly, the Kosciusko Island pack,

Table 7. Simplified habitat ranking matrix for wolf packs based on radio locations obtained before or after the pup-rearing period on Prince of Wales and Kosciusko islands in Southeast Alaska, USA. Matrix is based on results from logistic regression of radio locations compared with random locations. Signs indicate direction of selection and number of signs indicates significance of selection (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$). Scores for each category are derived by adding positive signs and multiplying by number of packs with positive signs, and then subtracting the sum of negative signs multiplied by number of packs with negative signs. Scores provide a qualitative comparison of direction and strength of habitat selection.

	Habitat Type[a]						
Pack	Lks	Ocog	Ccog	Seral	Ccut	Priv	Road
Ratz Harbor	+ + +		+				
Twin Spurs					–		
Honker Divide							
Kosciusko I.	+			– – –	– – –		
Kasaan Penin.							
Steelhead Crk.			+ +				
Thorne River			+	– –			

Scores	+8	0	+12	-10	-8	0	0

[a] Alpine habitat is excluded from analysis because it is strongly correlated with elevation. Codes for habitat types are as follows: Lks = lakes and streams, Ocog = open-canopy
old-growth forest and muskeg, Ccog = closed-canopy old-growth forest, Seral = second growth forest >25 years old, Ccut = second growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), and Road = road.

Table 8. Simplified habitat ranking matrix during winter for wolf packs on Prince of Wales and Kosciusko islands in Southeast Alaska, USA. Matrix is based on results from logistic regression of radio locations compared to random locations. Signs indicate direction of selection and number of signs indicates significance of selection (Three – $P \leq 0.05$, two – $0.05 < P \leq 0.1$, one – $0.1 < P \leq 0.15$). Scores for each category are derived by adding positive signs and multiplying by number of packs with positive signs, and then subtracting the sum of negative signs multiplied by number of packs with negative signs. Scores provide a qualitative comparison of direction and strength of habitat selection.

	Habitat Type [a]						
Pack [b]	Lks	Ocog	Ccog	Seral	Ccut	Priv	Road
Ratz Harbor			+ + +				
Twin Spurs							
Honker Divide		+ +	+ +				
Kosciusko I.		+					
Scores	0	+6	+10	0	0	0	0

[a] Alpine habitat is excluded from analysis because it is strongly correlated with elevation. Codes for habitat types are as follows: Lks = lakes and streams, Ocog = open-canopy

old-growth forest, Ccog = closed-canopy old-growth forest, Seral = second growth forest >25 years old, Ccut = second growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), and Road = road.

[b] Winter sample sizes for Kasaan Peninsula, Steelhead Creek, and Thorne River packs was too small to estimate habitat use.

Table 9. Simplified ranking matrix for measures of elevation and distance during winter for wolf packs on Prince of Wales and Kosciusko islands in Southeast Alaska, USA. Matrix is based on results from logistic regression of radio locations compared with random locations. Signs indicate direction of selection and number of signs indicates significance of selection (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$). Scores for each category are derived by adding positive signs and multiplying by number of packs with positive signs, and then subtracting the sum of negative signs multiplied by number of packs with negative signs. Scores provide a qualitative comparison of direction and strength of habitat selection.

	Elevation and Distance Measures		
Pack [a]	Elevation [b]	Dist. from Road [b]	Dist. from Lake or Stream [b]
Ratz Harbor	– – –		– –
Twin Spurs			– – –
Honker Divide	– –	– – –	
Kosciusko I.		– –	
Scores	-10	-10	-10

[a] Winter sample sizes for Kasaan Peninsula, Steelhead Creek, and Thorne River packs were too small to estimate habitat use.

[b] Negative signs indicate that radio locations were at lower elevation or closer to roads, lakes, and streams than matched random locations.

Table A-3. Results for stepwise logistic regression of habitat type, elevation, and distance measures for wolf packs on Prince of Wales and Kosciusko Islands, Southeast Alaska during the period before and after pup rearing. Results represent a comparison between radio locations of wolves (use) with matched random locations (available). Dashes indicate that the variable did not enter the model ($P > 0.15$).

Coefficients of Variables[a]

Wolf Pack	Elev.	Dist. Road	Dist. Lks	Lks	Ocog	Hvol	Seral	CCut	Priv	Road
Ratz Harbor	-0.023	-0.001	–	0.122	–	0.006	–	–	–	–
Twin Spurs	-0.002	-0.001	–	–	–	–	–	-0.004	–	–
Honker Divide	-0.005	-0.003	–	–	–	–	–	–	–	–
Kosciusko Island	–	-0.001	–	0.016	–	–	-0.031	-.025	–	–
Kasaan Peninsula	–	–	-0.003	–	–	-0.014	–	–	–	–
Steelhead Creek	–	–	–	–	–	0.014	–	–	–	-0.023
Thorne River	-0.014	-0.001	0.006	–	–	0.015	-0.031	–	–	–

P-values of Coefficients

Wolf Pack	Elev.	Dist. Road	Dist. Lks	Lks	Ocog	Ccog	Seral	CCut	Priv	Road
Ratz Harbor	0.044	0.096	–	0.052	–	0.148	–	–	–	–
Twin Spurs	0.017	0.110	–	–	–	–	–	0.126	–	–
Honker Divide	0.007	0.108	–	–	–	–	–	–	–	–
Kosciusko Island	–	0.002	–	0.038	–	–	0.011	0.009	–	–
Kasaan Peninsula	–	–	0.027	–	–	0.084	–	–	–	–
Steelhead Creek	–	–	–	–	–	0.094	–	–	–	0.110
Thorne River	0.006	0.146	0.047	–	–	0.150	0.050	–	–	–

Regression Diagnostics

Wolf Pack	*n*	Hosmer-Lemeshow Goodness-of-Fit	*P*	% Correct Classification
Ratz Harbor	63	9.93	0.270	62.6
Twin Spurs	194	7.60	0.474	57.3
Honker Divide	63	10.66	0.222	59.1
Kosciusko Island	50	6.37	0.605	70.0
Kasaan Peninsula	24	4.65	0.703	68.8
Steelhead Creek	20	2.12	0.713	65.0
Thorne River	22	6.83	0.555	79.6

a. Codes for variables are as follows: Elev. = elevation in meters, Dist. Road = distance from nearest road in meters, Dist. Lks = distance from nearest lake or stream in meters, Lks = lake or stream, Ocog = open-canopy old-growth forest or muskeg, Ccog = closed-canopy old-growth forest, Seral = second-growth forest >25 years old, Ccut = second-growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), Road = temporary and permanent road. Alpine habitat was excluded because it was strongly correlated with elevation.

Table A-4. Results for stepwise logistic regression of habitat type, elevation, and distance measures for wolf packs on Prince of Wales and Kosciusko Islands, Southeast Alaska during winter. Results represent a comparison between radio locations of wolves (use) with matched random locations (available). Dashes indicate that the variable did not enter the model ($P > 0.15$).

Coefficients of Variables[a]

Wolf Pack	Elev.	Dist. Road	Dist. Lks	Lks	Ocog	Hvol	Seral	CCut	Priv	Road
Ratz Harbor	-0.048	–	-0.001	–	–	0.014	–	–	–	–
Twin Spurs	–	–	-0.002	–	–	–	–	–	–	–
Honker Divide	-0.004	-0.001	–	–	0.012	0.011	–	–	–	–
Kosciusko Island	–	-0.001	–	–	0.013	–	–	–	–	–

P-values of Coefficients

Wolf Pack	Elev.	Dist. Road	Dist. Lks	Lks	Ocog	Ccog	Seral	CCut	Priv	Road
Ratz Harbor	0.020	–	0.136	–	–	0.044	–	–	–	–
Twin Spurs	–	–	0.008	–	–	–	–	–	–	–
Honker Divide	0.086	0.020	–	–	0.088	0.072	–	–	–	–
Kosciusko Island	–	0.053	–	–	0.116	–	–	–	–	–

Regression Diagnostics

Wolf Pack	*n*	Hosmer-Lemeshow Goodness-of-Fit	*P*	% Correct Classification
Ratz Harbor	30	12.62	0.082	76.1
Twin Spurs	114	6.19	0.517	55.7
Honker Divide	40	8.57	0.379	68.8
Kosciusko Island	20	10.19	0.251	55.0

a. Codes for variables are as follows: Elev. = elevation in meters, Dist. Road = distance from nearest road in meters, Dist. Lks = distance from nearest lake or stream in meters, Lks = lake or stream, Ocog = open-canopy old-growth forest or muskeg, Ccog = closed-canopy old-growth forest, Seral = second-growth forest >25 years old, Ccut = second-growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), Road = temporary and permanent road. Alpine habitat was excluded because it was strongly correlated with elevation.

which showed weak evidence of selection for open-canopy old growth, also occupied an area of low snowfall. In contrast, home ranges of the Honker Divide and Ratz Harbor packs mostly overlapped areas where snow depth exceeded 60 cm.

Wolf packs typically were located nearer to roads than matched random locations regardless of season (Tables 4 and 6). Nonetheless, that outcome may have resulted from wolves spending most of their time at low elevation, which also was where road density was highest ($r = -0.83$, $P = 0.001$, Fig. 10). To reduce the confounding influence of elevation, we constrained data to only those locations <100 m in elevation, and then repeated our analysis of habitat selection. Wolves at low elevations strongly selected closed-canopy and open-canopy old-growth forest, while avoiding clearcuts and roads (Tables 10 and 11, Table A-5). Further, wolves showed a strong affinity for habitats that were closer to lakes and streams. Two wolf packs selected for habitats near roads but no packs selected roads; 3 of 7 packs avoided roads. The explanation for that paradox was that wolves frequently used logged landscapes, but selected for unlogged areas within those landscapes.

Relations between habitat, activity, and time of day.—Wolves were significantly more active during night than day (Fig. 11). That pattern was consistent in all packs for which nighttime locations were available. We compared habitat use of active wolves with that of inactive wolves using Kruskal-Wallis tests. We combined seasons because the sample of nighttime locations was too small to allow that stratification. The most consistent pattern among the 7 packs monitored was that they were more active near clearcuts or on roads (Tables 12 and 13). Activity was associated with unclassified

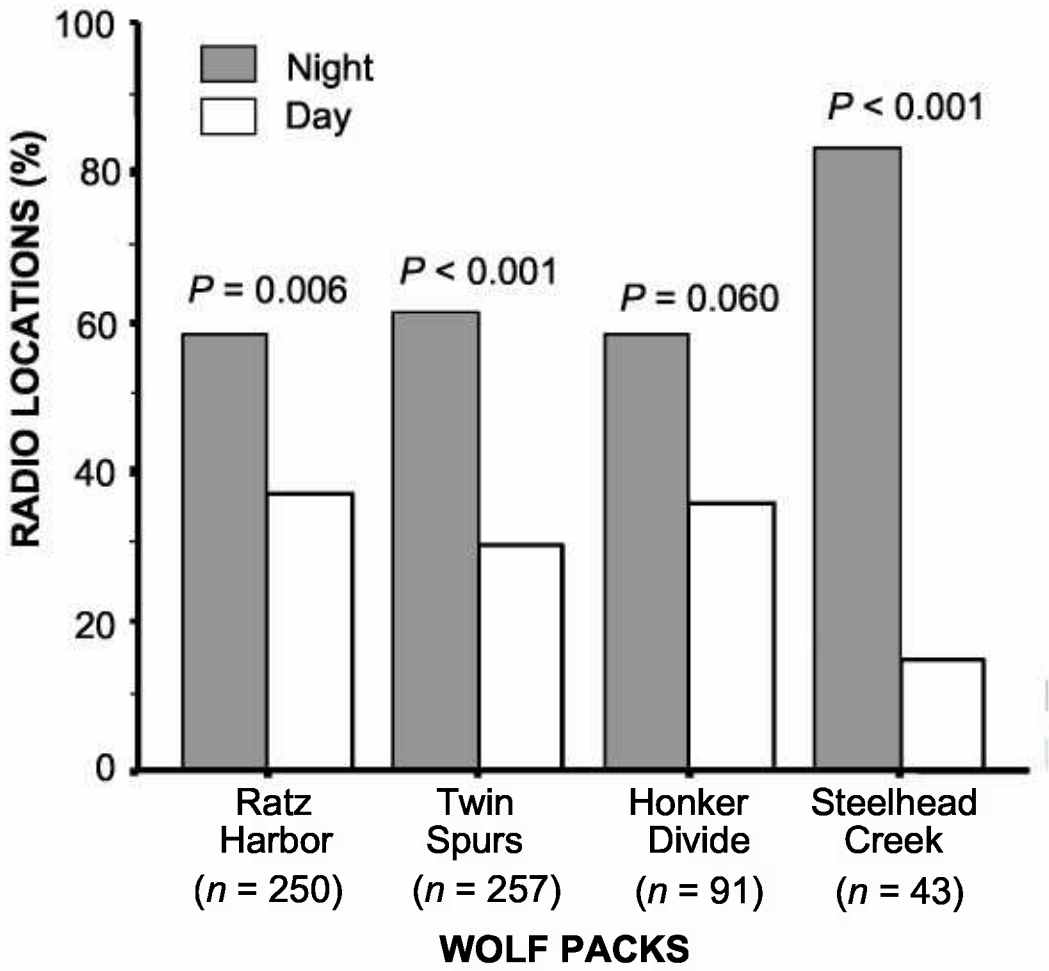

Figure 11. Percentage of radio locations for active wolves during day and night on Prince of Wales and adjacent islands, Southeast Alaska, USA. Exact *P*-values for chi-square tests of independence between daytime and nighttime radio locations are shown.

Table 10. Simplified habitat ranking matrix for all radio locations and random locations ≤100m elevation obtained for wolves on Prince of Wales and Kosciuko islands in Southeast Alaska, USA. Matrix is based on results from logistic regression of radio locations compared with random locations. Signs indicate direction of selection and number of signs indicates significance of selection (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$). Scores for each category are derived by adding positive signs and multiplying by number of packs with positive signs, and then subtracting the sum of negative signs multiplied by number of packs with negative signs. Scores provide a qualitative comparison of direction and strength of habitat selection.

	Habitat Type[a]						
Pack	Lks	Ocog	Ccog	Seral	Ccut	Priv	Road
Ratz Harbor			+ + +		– – –		– – –
Twin Spurs		+ + +	+				– – –
Honker Divide		+ + +					
Kosciusko I.							
Kasaan Penin.		+ + +	+ + +			+ +	
Steelhead Crk.			+ + +		– – –		–
Thorne River	– – –						

Score	-3	+27	+40	0	-12	+2	-21

[a] Codes for habitat types are as follows: Lks = lakes and streams, Ocog = open-canopy old-growth forest and muskeg, Ccog = closed-canopy old-growth forest, Seral = second growth forest >25 years old, Ccut = second growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), and Road = road.

Table 11. Simplified ranking matrix of elevation and distance measures for all radio locations and random locations ≤100m elevation obtained for wolves on Prince of Wales and Kosciuko islands in Southeast Alaska, USA. Matrix is based on results from logistic regression of radio locations compared with random locations. Signs indicate direction of selection and number of signs indicates significance of selection (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$). Scores for each category are derived by adding positive signs and multiplying by number of packs with positive signs, and then subtracting the sum of negative signs multiplied by number of packs with negative signs. Scores provide a qualitative comparison of direction and strength of habitat selection.

	Elevation and Distance Measures		
Pack	Elevation[a]	Dist. from Road[a]	Dist. from Lake or Stream[a]
Ratz Harbor		– – –	– –
Twin Spurs			– – –
Honker Divide		– – –	
Kosciusko I.			– – –
Kasaan Penin.			
Steelhead Crk.			– – –
Thorne River			

Scores	0	-12	-44

[a] Negative signs indicate that radio locations were at lower elevation or closer to roads, lakes, and streams than matched random locations.

Table 12. Simplified habitat ranking matrix comparing periods of activity and resting for wolf packs on Prince of Wales and Kosciuko islands in Southeast Alaska, USA. Matrix is based on results from Kruskal-Wallis tests of radio locations. All biological seasons are combined. An "a" indicates that habitat ranked higher when wolves were active than when they were resting. Number of letters indicates significance of difference between active and resting (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$).

	Habitat Type[a]						
Pack	Lks	Ocog	Ccog	Seral	Ccut	Priv	Road
Ratz Harbor	a		a a a		a a		a
Twin Spurs				a a a	a a a		
Honker Divide					a a a		a a a
Kosciusko I.	a a a				a a		a a a
Kasaan Penin.						a a	
Steelhead Crk.							
Thorne River	a						

[a] Alpine habitat is excluded from analysis because it is strongly correlated with elevation. Codes for habitat types are as follows: Lks = lakes and streams, Ocog = open-canopy

old-growth forest and muskeg, Ccog = closed-canopy old-growth forest, Seral = second growth forest >25 years old, Ccut = second growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), and Road = road.

Table 13. Simplified ranking matrix of elevation and distance measures comparing periods of activity and resting for wolf packs on Prince of Wales and Kosciuko islands in Southeast Alaska, USA. Matrix is based on results from Kruskal-Wallis tests of radio locations. All biological seasons are combined. An "r" indicates that habitat ranked higher when wolves were resting. Number of letters indicates significance of difference between active and resting (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$).

	Elevation and Distance Measures		
Pack	Elevation[a]	Dist. from Road[a]	Dist. from Lake or Stream[a]
Ratz Harbor			
Twin Spurs		r r r	
Honker Divide		r r r	
Kosciusko I.	r r r		
Kasaan Penin.			
Steelhead Crk.		r r r	
Thorne River			

[a] An "a" indicates active at higher elevation or further from roads, lakes, and streams. An "r" indicates resting at higher elevation or further from road, lakes, and streams.

Table A-5. Results for stepwise logistic regression of habitat type, elevation, and distance measures for wolf packs on Prince of Wales and Kosciusko Islands, Southeast Alaska. Results represent a comparison between all radio locations of wolves (use) ≤100 m elevation and matched random locations (available). Dashes indicate that the variable did not enter the model ($P > 0.15$).

Coefficients of Variables[a]

Wolf Pack	Elev.	Dist. Road	Dist. Lks	Lks	Ocog	Hvol	Seral	CCut	Priv	Road
Ratz Harbor	–	-0.002	-0.001	–	–	0.009	–	-0.011	–	-0.013
Twin Spurs	–	–	-0.001	–	0.007	0.004	–	–	–	-0.014
Honker Divide	–	-0.004	–	–	0.012	–	–	–	–	–
Kosciusko Island	–	–	-0.003	–	–	–	–	–	–	–
Kasaan Peninsula	–	–	–	–	0.032	0.033	–	–	0.023	–
Steelhead Creek	–	–	-0.002	–	–	0.025	–	-0.029	–	-0.024
Thorne River	–	–	–	-0.024	–	–	–	–	–	–

P-values of Coefficients

Wolf Pack	Elev.	Dist. Road	Dist. Lks	Lks	Ocog	Ccog	Seral	CCut	Priv	Road
Ratz Harbor	–	0.000	0.067	–	–	0.023	–	0.046	–	0.019
Twin Spurs	–	–	0.046	–	0.008	0.150	–	–	–	0.007
Honker Divide	–	0.046	–	–	0.041	–	–	–	–	–
Kosciusko Island	–	–	0.006	–	–	–	–	–	–	–
Kasaan Peninsula	–	–	–	–	0.006	0.020	–	–	0.052	–
Steelhead Creek	–	–	0.043	–	–	0.021	–	0.013	–	0.111
Thorne River	–	–	–	0.047	–	–	–	–	–	–

Regression Diagnostics

Wolf Pack	*n*	Hosmer-Lemeshow Goodness-of-Fit	*P*	% Correct Classification
Ratz Harbor	111	5.09	0.747	74.0
Twin Spurs	216	3.94	0.863	66.0
Honker Divide	44	8.89	0.352	65.8
Kosciusko Island	79	5.18	0.638	75.8
Kasaan Peninsula	21	6.60	0.158	69.8
Steelhead Creek	17	8.16	0.418	76.3
Thorne River	26	7.43	0.059	79.5

a. Codes for variables are as follows: Elev. = elevation in meters, Dist. Road = distance from nearest road in meters, Dist. Lks = distance from nearest lake or stream in meters, Lks = lake or stream, Ocog = open-canopy old-growth forest or muskeg, Ccog = closed-canopy old-growth forest, Seral = second-growth forest >25 years old, Ccut = second-growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), Road = temporary and permanent road.

private lands for the Kasaan Peninsula pack. Most of those lands were composed of clearcuts indicating that the pattern of activity for that pack was similar to the others. Three packs were more active when near lakes and streams, and 3 packs rested further from roads than when active.

Four packs had sufficient numbers of radio locations during the night for us to assess diurnal differences in habitat use. Wolves used seral forest, clearcuts, and roads more often at night than during the day (Table 14). Private lands, which were mostly composed of clearcuts, were used by 2 packs more often at night. Wolves used habitat closer to roads at night, which also was consistent with their use of logged habitat (Table 15). Daytime locations were more often in open-canopy or closed-canopy old-growth forest. We conclude that wolves used habitats associated with logging mostly when they were active at night.

Relation between habitat, home range, and pack size.—We hypothesized that home range for a pack of wolves would be influenced by amount and dispersion of critical habitat for deer in winter. Home range, however, was strongly correlated with pack size; thus comparisons among pack home ranges must first be adjusted for number of wolves within each pack. We did this by dividing home-range size by the number of wolves in a pack during late summer (when pack size was largest). We termed this ratio the

home-range index (Table 16). We predicted that the home-range index would be small if the proportion of deer habitat was large and was less widely dispersed. We regressed home-range index against the proportion of winter habitat for deer within the home

Table 14. Simplified habitat ranking matrix comparing daytime and nighttime locations for wolf packs on Prince of Wales and Kosciuko islands in Southeast Alaska, USA. Matrix is based on results from Kruskal-Wallis tests of radio locations. All biological seasons are combined. A "d" indicates that habitat ranked higher for daytime locations when compared to nighttime locations. An "n" indicates that habitat ranked higher for nighttime locations when compared to daytime locations. Number of letters indicates significance of difference between daytime and nighttime (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$).

	Habitat Type[a]						
Pack[b]	Lks	Ocog	Ccog	Seral	Ccut	Priv	Road
Ratz Harbor		d d d		n n n	n n		
Twin Spurs							
Honker Divide			d d	n n n	n n n	n n	n n n
Steelhead Crk.		d d d			n n	n n n	

[a] Alpine habitat is excluded from analysis because it is strongly correlated with elevation. Codes for habitat types are as follows: Lks = lakes and streams, Ocog = open-canopy

old-growth forest and muskeg, Ccog = closed-canopy old-growth forest, Seral = second growth forest >25 years old, Ccut = second growth forest ≤25 years old, Priv = unspecified private land (mostly Ccut), and Road = road.

[b] Kosciusko Island, Kasaan Peninsula, and Thorne River packs had nighttime sample sizes that were too small for comparison.

Table 15. Simplified ranking matrix of elevation and distance measures comparing daytime and nighttime locations for wolf packs on Prince of Wales and Kosciuko islands in Southeast Alaska, USA. Matrix is based on results from Kruskal-Wallis tests of radio locations. All biological seasons are combined. A "d" indicates that daytime locations were at higher elevations or further from roads, lakes, and streams. An "n" indicates that nighttime locations were at higher elevations or further from road, lakes, and streams. Number of letters indicates significance of difference between daytime and nighttime (Three = $P \leq 0.05$, two = $0.05 < P \leq 0.1$, one = $0.1 < P \leq 0.15$).

	Elevation and Distance Measures		
Pack [a]	Elevation	Dist. from Road	Dist. from Lake or Stream
Ratz Harbor	d d	d d d	d d d
Twin Spurs			
Honker Divide		d d d	n n n
Steelhead Crk.		d d d	

[a] Kosciusko Island, Kasaan Peninsula, and Thorne River packs had nighttime sample sizes that were too small for comparison.

Table 16. Home range, average pack size, and home range index for wolf packs on Prince of Wales and Kosciusko islands in Southeast Alaska, USA. Also shown are measures of area and dispersion of critical winter habitat for deer within wolf home ranges.

Pack	Home Range[a] (km^2)	Pack Size[b]	Home-Range Index[c]	Deer Habitat[d]	Standard Radius[e]
Ratz Harbor	394.3	7	56.3	4.7	11.3
Twin Spurs	353.6	8	44.2	9.2	10.7
Honker Divide	353.8	12	29.5	11.7	8.5
Kosciusko Island	329.0	7	47.0	10.8	9.2
Kasaan Peninsula	150.8	4	37.7	3.6	6.9
Steelhead Creek	153.6	3	51.2	3.1	6.8
Thorne River	82.6	4	20.7	18.7	3.8
Mean	259.7	6.4	40.9	8.8	8.1
SE	47.5	1.2	4.7	2.1	2.6

[a] Mohr's convex polygon home ranges.

[b] Pack size in late summer averaged over number of years that data are available.

[c] Home range ÷ pack size.

[d] Percentage of home range composed of critical winter habitat for deer.

[e] Standard radius (km), a measure of dispersion of deer winter habitat about the weighted mean center of each wolf pack's home range. It is analogous to a standard deviation for nonspatial data.

range and the standardized distance of patches of deer habitat from the geographic mean center of the home range (a measure of dispersion) (Table 16). Results indicated that the home-range index was strongly influenced by proportion of winter habitat for deer within the home range (Table 17). Dispersion of winter habitat for deer, however, did not influence the home-range index significantly ($t_5 = -1.347$, $P = 0.249$). Next, we added the proportions of home ranges that were clearcuts and seral forest as independent variables along with winter habitat for deer. The resulting regression included the same negative term for percentage of deer habitat, and added a positive term for seral forest (Table 17). Those results support the notion that critical winter habitat for deer is a good measure of habitat quality for wolves, and may be an indicator of the availability of deer within home ranges of wolf packs. Conversely, presence of seral forest within the home range of a wolf pack may increase the size of the home range because that habitat is poor for deer.

Pack size should be influenced by the amounts of seral forest and winter habitat for deer within the home range of a pack, if those variables are measures of habitat quality. We regressed pack size (averaged over the number of years a pack was monitored) against hectares of deer habitat and seral forest within home ranges. Pack size was positively correlated with the area of winter habitat for deer ($t_6 = 4.18$, $P = 0.009$; Fig. 12) but not correlated with seral forest ($t_6 = -0.23$, $P = 0.831$).

Interactions between habitat and wolf mortality.—To examine the relation between habitat and mortality of wolves, we compared average distance from roads, frequency of use of closed-canopy old-growth forest, and frequency of use of clearcuts for radio

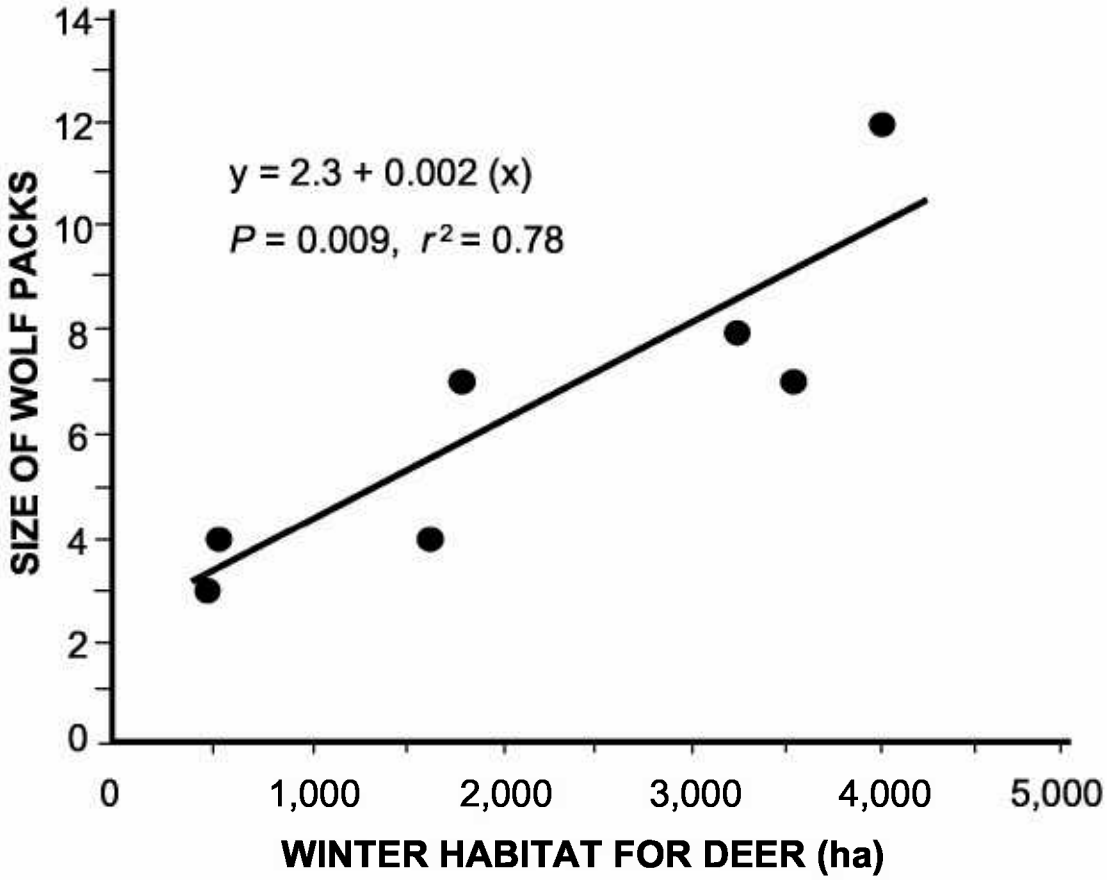

Figure 12. Regression of size of packs in autumn for 7 wolf packs versus hectares of critical winter habitat for deer within wolf pack home ranges on Prince of Wales and Kosciusko islands, Southeast Alaska, USA.

Table 17. Results from stepwise multiple linear regression[a] of home range index as the dependent variable and percent of winter habitat for deer and seral forest within pack home ranges as independent variables. Data are from wolves on Prince of Wales and Kosciusko islands in Southeast Alaska, USA.

Variable	Coefficient	*t*	*P*
Constant	4980.61	11.17	0.000
Percent deer habitat	-160.33	-4.06	0.015
Percent seral forest	96.44	2.88	0.045

[a] $r^2 = 0.80$, $F = 12.71$, $P = 0.018$

locations of wolves that survived with those that died. We believed that those variables would contribute to the survival or death of wolves directly. Wolves that avoided roads or that stayed hidden in closed-canopy old-growth forest would be less likely to be shot or trapped. Conversely, wolves that frequently used clearcuts would be more likely to be seen and killed by hunters and trappers. Results indicated that wolves that died were located closer to roads and less often in closed-canopy old growth (Fig. 13). There was no significant relation between death of wolves and use of clearcuts (Fig. 13).

Roads and wolf mortality.— We examined mortality within packs of wolves that were monitored, as well as analyzing harvest data obtained by the Alaska Department of Fish and Game. We tallied wolves that were harvested within the areas defined by the home ranges of wolf packs that we monitored to reconstruct mortality incurred by each pack. We then compared average harvest of wolves per pack between 1993 and 1995 with home-range size, density of roads within the home range, and distance of the geographic center of the home range to the nearest town. Average harvest per pack was positively related to size of the home range and density of roads within the home range, but not to the average distance from towns (Table 18). Standardized regression coefficients indicated that density of roads had the most influence on average harvest.

We compiled harvest data on wolves for all wildlife analysis areas in game management unit 2 for 1990–98 (Alaska Department of Fish and Game, *unpublished data*). About 53% of total harvest was accounted for by humans trapping or hunting from boats (Table 3). Hunters and trappers that gained access to wolves from roads accounted for 44% of the total kill ($n = 851$). We compared those harvest data with the

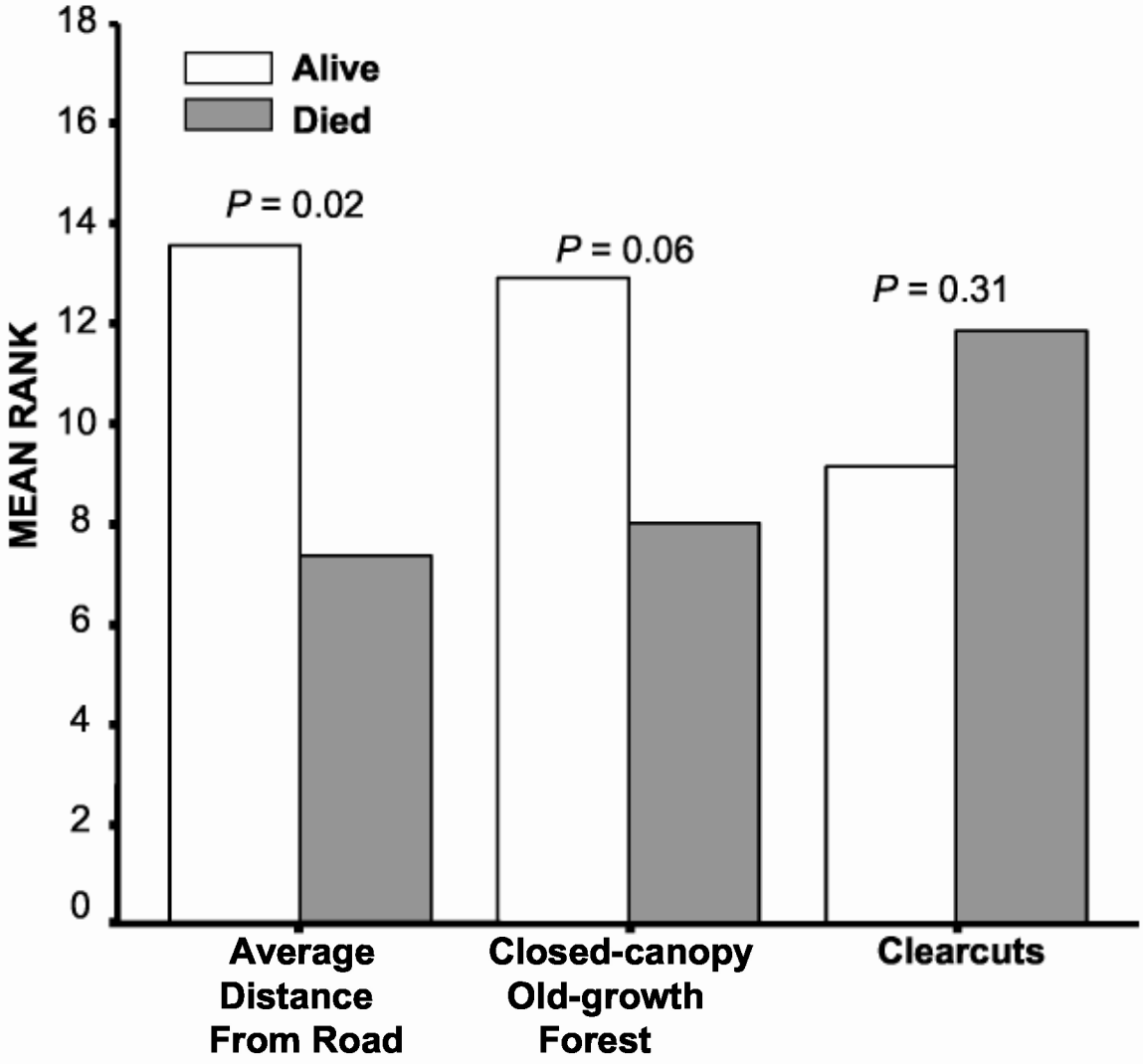

Figure 13. Results from Mann-Whitney *U* tests comparing mean ranks of several habitat variables for resident wolves that died with those that survived. Data are from 15 resident wolves monitored on Prince of Wales and Kosciusko islands in Southeast Alaska, USA, between March 1993 and September 1995.

Table 18. Results from stepwise multiple linear regression[a] of harvest of wolves within a pack as the dependent variable and home ranges, density of roads within home ranges, dispersion of roads within home ranges, and average distance of geographic centers of home ranges from towns. Harvest data are averaged for years 1993–95. Data are from wolves on Prince of Wales and Kosciusko islands in Southeast Alaska, USA.

Variable	Coefficient	t	P
Constant	-1.220	-1.284	0.268
Home Range	0.006	3.18	0.033
Road Density	2.893	3.097	0.036
Standard Radius	-0.309	-0.522	0.638
Distance From Town	0.319	1.761	0.177

[a] $r^2 = 0.74$, $F = 9.48$, $P = 0.030$

size of wildlife analysis areas, length of roads, density of roads, and average distance of geographic centers from towns. We also included the habitat suitability index for deer developed by the U. S. Forest Service, which served as a analog for relative quality of habitat within wildlife analysis areas. Vehicular traffic was much greater on roads connected to the main road system on Prince of Wales Island and the ferry system that enabled access to the island. Therefore, we included a binary variable that indicated whether a wildlife analysis area was connected to the main road system.

The average harvest for wildlife analysis areas connected to the main road system was 4.1 wolves and was much higher than the average of 1.3 wolves for wildlife analysis areas that were not connected by the road system (Mann-Whitney $U = 11.5$, exact $P < 0.001$, $n = 26$). Because of that large difference, we chose to treat wildlife analysis areas that were connected to the main road system separately from those that were not. Many wildlife analysis areas were accessible by both vehicle and boat, and wolves were harvested by hunters and trappers using both means of conveyance. We excluded those wolves killed by hunters and trappers from boats, and focused only on those wolves killed from the road system.

We used multiple regression to relate the average harvest of wolves from roads in wildlife analysis areas to the sizes of wildlife analysis areas, lengths of roads within the areas, and average geographic distances from towns. Logically, we forced the regression model through the origin because there could be no harvest from roads if none existed. For all wildlife analysis areas, length of roads was the only variable that related significantly to average harvest of wolves (Table 19), regardless of their

Table 19. Results from stepwise multiple linear regression[a] of harvest of wolves from roads for wildlife analysis areas in game management unit 2. Average harvest for a wildlife analysis area between 1990 and 1998 is the dependent variable and length of roads in wildlife analysis areas, size of wildlife analysis areas, and average distance of geographic centers of wildlife analysis areas from towns are independent variables. Results are shown for wildlife analysis areas connected to the main road system on Prince of Wales Island and for those that are not connected. Game management unit 2 includes Prince of Wales and adjacent islands in Southeast Alaska, USA.

Variable	Coefficient	*t*	*P*
Connected			
Length of Road	0.009	9.099	0.000
Size of Area	-0.320	-1.384	0.194
Distance From Town	0.146	0.864	0.406
Not Connected			
Length of Road	0.002	3.877	0.001
Size of Area	0.044	0.200	0.844
Distance From Town	0.222	1.073	0.300

[a] Regression for connected: $r^2 = 0.87 F = 82.79$, $P < 0.000$; for not connected: $r^2 = 0.484$, $F = 15.03$, $P < 0.001$.

connection to the main road system on Prince of Wales Island. Size of wildlife analysis areas was not a factor influencing harvest, which was surprising. Consequently, length of road in a wildlife analysis area may be a reasonable predictor of how many wolves will be killed during hunting and trapping seasons, regardless of size of that area.

Not surprisingly, the coefficient for length of roads was smaller for those wildlife analysis areas not connected to the main road system. Indeed, vehicle traffic was limited in those areas because of the expense in transporting vehicles to them. Nonetheless, the coefficient for length of roads was significantly different than 0 ($P = 0.001$), indicating that roads had a measurable effect on harvest of wolves in wildlife analysis areas not connected to the main road system. Fisherman and hunters often transported 3- and 4-wheeler off-road vehicles by boat to those areas, and vehicles usually were present at logging camps. We repeated our analyses substituting density of roads within wildlife analysis areas for lengths of roads and sizes of wildlife analysis areas. Density of roads was a significant indicator of harvest in wildlife analysis areas whether connected or unconnected to the main road system (Table 20). The lower coefficient of determination (r^2) for density of roads indicated, however, that length of roads may be a better predictor.

We created a binary variable to represent harvest in a wildlife analysis area above or below the sustainable harvest rate for wolves (28%), and used logistic regression to relate that variable to density of roads within wildlife analysis areas, geographic distances of the wildlife analysis areas from towns, and connection of wildlife analysis areas to the main road system on Prince of Wales Island. The best-fitting model

Table 20. Results from stepwise multiple linear regression[a] of harvest of wolves from roads for wildlife analysis areas in game management unit 2. Average harvest for a wildlife analysis area between 1990 and 1998 is the dependent variable and density of roads in wildlife analysis areas, and average distances of geographic centers of wildlife analysis areas from towns are independent variables. Results are shown for wildlife analysis areas connected to the main road system on Prince of Wales Island and for those that are not connected. Game management unit 2 includes Prince of Wales and adjacent islands in Southeast Alaska, USA.

Variable	Coefficient	*t*	*P*
Connected			
Density of Road	3.366	7.683	0.000
Distance From Town	0.058	0.247	0.809
Not Connected			
Density of Road	0.398	4.967	0.000
Distance From Town	0.211	1.226	0.239

[a] Regression for connected: $r^2 = 0.831$, $F = 59.03$, $P = 0.000$; for not connected: $r^2 = 0.607$,

$F = 24.67$, $P = 0.000$.

included terms for density of roads, distance from towns, and an interaction term for distance from towns and connection to the main road system (Table 21). We used the model:

Ln(probability of unsustainable harvest = 1) = 2.16(density of roads) + 0.255(distance from towns) – 0.198(distance from towns × connection to main road system) – 4.497

to predict density of roads at which there was a 50% probability that unsustainable harvest of wolves would occur. We estimated that a density of roads ≥0.53 km/km^2 for wildlife analysis areas connected to the main road system would likely result in overharvesting wolves. For wildlife analysis areas that were not connected to the main road system, the limit for density of roads was 1.04 km/ km^2. We emphasize that density of roads used in these calculations includes all existing roads regardless of whether they were closed to vehicular traffic.

Predator-prey Modeling

Application of the wolf-deer model to Isle Royale and Coronation Island.—To simulate conditions on Isle Royale, we divided the island into 2 permanent pack areas that shared the population of moose equally. This divided the wolf population into 2 distinct groups that were linked by dispersal. Large pack sizes and numbers of pups predicted by the model can be interpreted as the result of permanent packs temporarily splitting and increasing the number of breeding females. We parameterized the ungulate portion of the model as follows:

Table 21. Results from stepwise logistic regression[a] of probability of overharvesting wolves in a wildlife analysis area as the dependent variable and density of roads within wildlife analysis areas, average distances of geographic centers of wildlife analysis areas from towns, and interaction between distances from towns and if wildlife analysis areas are connected to the main road system on Prince of Wales Island as independent variables. Data are from wolves in game management unit 2, which includes Prince of Wales and adjacent islands in Southeast Alaska, USA.

Variable	Coefficient	S.E	*P*
Road Density	2.163	1.129	0.055
Distance From Town	0.255	0.116	0.028
Distance From Town x Connect	-0.198	0.092	0.031

[a] Hosmer and Lemeshow Goodness of Fit $\chi^2 = 5.82$, $df = 8$, $P = 0.667$, Correct Classification = 80.0%.

$K = 2{,}000$ moose, which is about 200 moose higher than the population reported by DelGiudice et al. (1997),

$U_0 = 0.75(K)$, the model is insensitive to initial conditions so this value is arbitrary,

$C = N(9, 1.4)$ (Keith 1983),

$r = 0.40$ (Cederland and Sand 1994, Bowyer et al. 1999),

$\theta = U(1,3)$, and

$\alpha = U(0.25, 0.75)$.

Vulnerability of moose to predation is age-specific (Peterson and Page 1988), therefore, we allowed the parameter representing percentage of the moose population available to wolves to vary uniformly between 25-75%; a lower range than that used in simulations for deer. Actual availability of ungulate prey is a complex factor involving weather, age structure, habitat, and behavior. We cannot hope to measure all influences simultaneously, yet it is highly unlikely that 100% of an ungulate population is available to wolves. We gave this parameter a wide uniform distribution in all of our simulations to reflect the uncertainty surrounding that value. We simulated winters with an average frequency of 1 severe winter per decade.

The parameters used in the wolf model were:

$P_0 = 2$ wolves (the initial colonizing pair),

$S_t = N(4,2)$ (Peterson and Page 1988, Fuller 1989),

$d = N(0.5,0.15)$ (Peterson and Page 1988),

$s_d = N(0.5, 0.15)$ (Peterson et al 1984, Fuller 1989), and

$m = N(0.5, 0.15)$ (Peterson and Page 1988).

Dispersal only was allowed between pack areas and not from the island. Immigration and mortality from hunting and trapping were set at 0.

Beginning with a single pair of wolves, moose and wolf populations on Isle Royale were simulated for a 50-year period 2,000 times with Monte Carlo techniques (Fig. 14). The mean wolf population in spring (before pups were born) after 3 years was 13 animals (populations in autumn were about 20-30% larger). After the first 20 years, the mean population in spring was 24 wolves. The maximum number of wolves predicted for any particular year was 53 and the minimum was 0. Only 1% of simulated populations, however, went extinct during the 50-year period. The mean preparturient population of moose after 20 years was 1,432 animals and the range was 45–2,000 moose.

Actual late-winter populations of wolves on Isle Royale generally have ranged between 14 and 25 wolves with a short-lived population surge occurring in the late 1970s (Mech 1970, Peterson and Page 1988). The population reached a maximum of 50 wolves in 1980 and then crashed to 14 wolves by 1983. Mean populations predicted by our wolf-deer model are close to actual population levels. Moose populations on Isle Royale fluctuated dramatically between 1960 and 1995, with lows of about 500 animals and highs close to 2,000 (DelGiudice et al. 1997). The mean population for the last 20 years has been well above 1,000 moose in winter, which is consistent with predictions from our model.

We simulated wolf and deer populations on Coronation Island by setting K for deer at 600 animals and introducing a population of 4 wolves. Our estimate of K was based

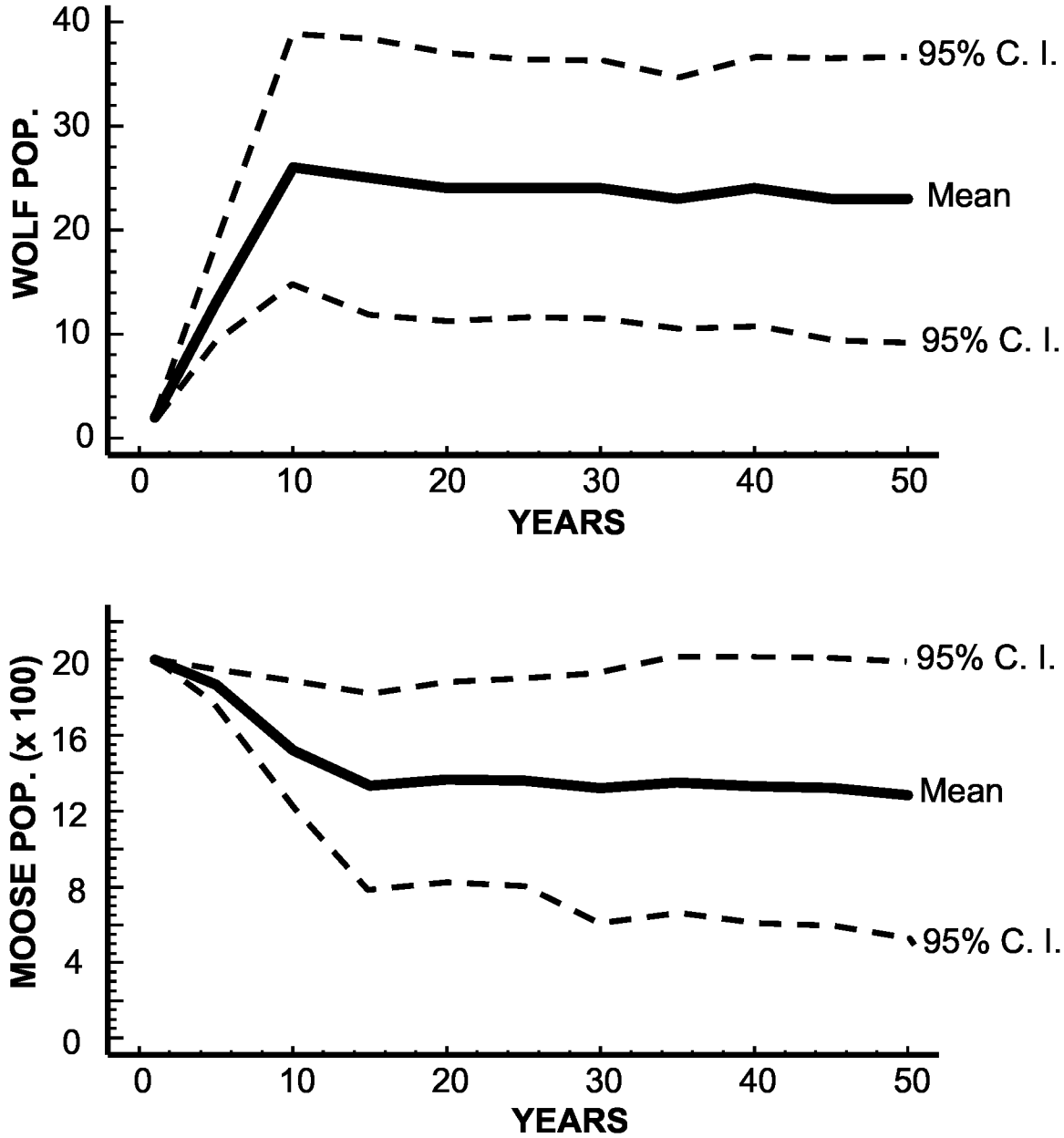

Figure 14. Results of Monte Carlo simulations (n = 2,000) of our wolf-deer model applied to Isle Royale, Michigan, USA. Model was parameterized with values appropriate for wolves and moose (Keith 1983, Peterson and Page 1988, Fuller 1989, Cederland and Sand 1991, Delguidice 1997, Bowyer et al. 1999). Simulations began with a pair of wolves and assumed wolf and moose populations were isolated on Isle Royale.

on the maximum number of deer estimated to be on the island in 1960 by Klein (1995). Evidence of severe browsing suggested to Klein (1995) that deer were near K in 1960, before wolves were introduced. A single wolf pack would occupy the entire island, therefore, only 1 pack area was modeled. The deer portion of our model was parameterized as follows:

$K = 600$ deer,

$U_0 = 600$, (Klein 1995),

$C = N(26, 4)$ (Person et al. 1996),

$r = 0.6$, value suggested for mule deer (*Odocoileus hemionus;* McCullough 1987),

$\theta = U(1,3)$, and

$\alpha = U(0.5, 0.9)$.

We sampled the parameter α from a uniform distribution with a wide range because of the uncertainty surrounding that value.

The following parameters were used in the wolf portion of the model:

$P_0 = 4$ wolves (the initial colonizing pairs),

$S_t = N(4,2)$, based on data from this study, and

$m = N(0.5, 0.15)$ (Peterson et al. 1984).

Immigration and dispersal to and from the island were not allowed. During the first year of the field experiment, 2 of the introduced wolves were shot (Klein 1995), and another was introduced in the third year of the experiment. We accounted for that loss and addition in our simulation, but allowed no hunting or trapping mortality to occur in subsequent years.

Monte Carlo simulations (n = 2,000) of our model for Coronation Island showed the number of wolves increasing from an initial population of 4 animals to a mean population of 13 wolves in 4 years, followed by a precipitous decline to extinction (Fig. 15). Deer numbers declined dramatically after wolves were introduced and irrupted when wolves disappeared. The actual population of wolves also took 4 years to reach a peak of 13 animals and then declined to 1 wolf 3 years later (Klein 1995). This last animal may have persisted for 2 or 3 years after the decline. The deer population was reduced in 3 years to a point at which investigators could find little evidence of their presence on the island (Klein 1995). After the wolves disappeared, the deer population on Coronation Island rebounded to a level at which they again approached K (Lewis 1992).

Our model predictions were reasonably consistent with empirical data from Isle Royale and Coronation Island. Populations predicted by our model tended to fluctuate more widely than actual populations because the probability distributions of input parameters incorporated greater variability than would occur in most real populations. Standard errors of input parameters reflect intrinsic variability as well as uncertainty associated with the means of the distributions owing to limited data.

Application of the model to Prince of Wales and adjacent islands.—We used our model to simulate the wolf-deer system on Prince of Wales and adjacent islands (game management unit 2) for a 90-year period beginning in 1955 and ending in 2045. We estimated number of pack areas in game management unit 2 by dividing total land area below 400 m in elevation by the average area below 400 m within home ranges for wolf

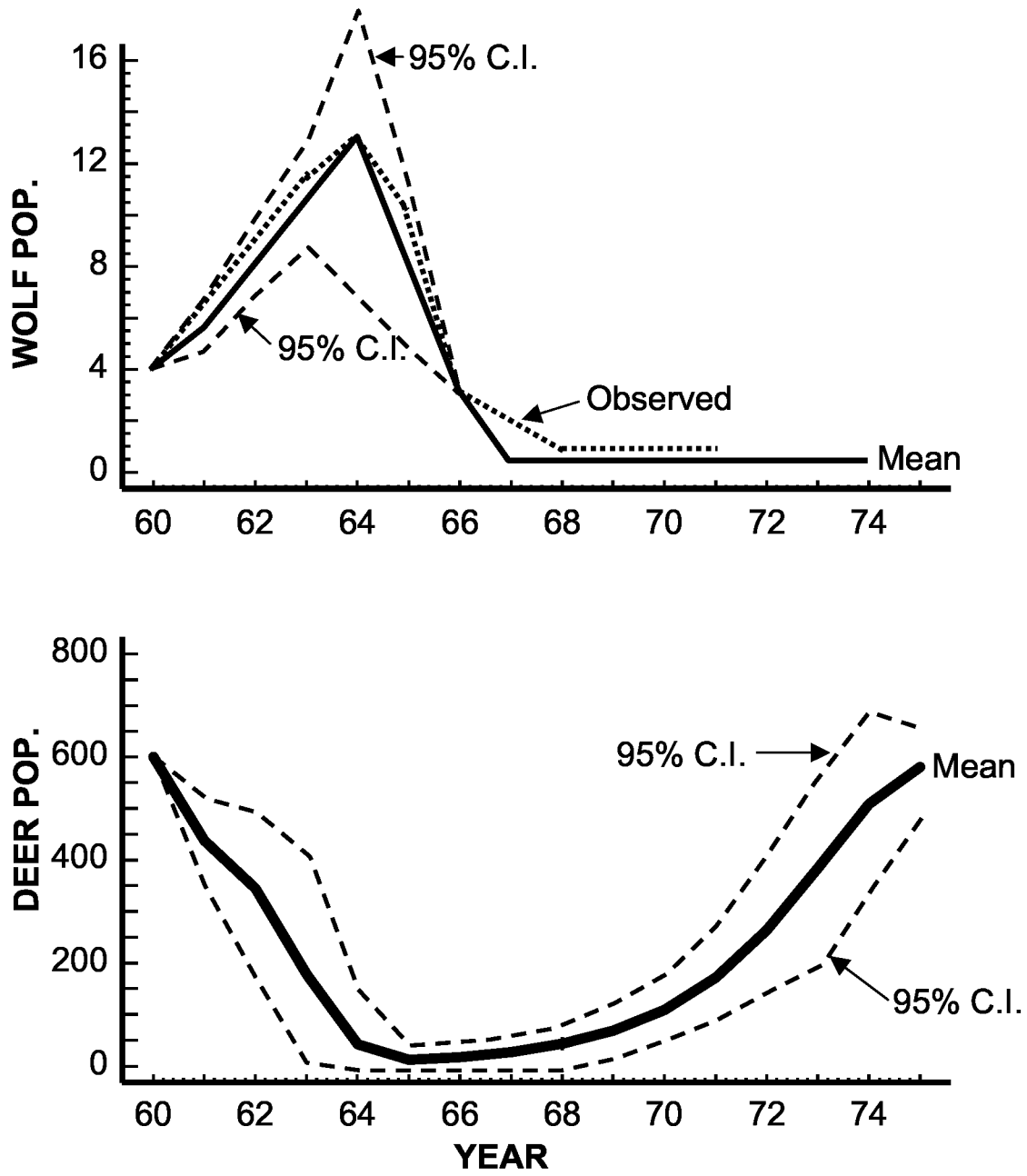

Figure 15. Results of Monte Carlo simulations (n = 2,000) of our wolf-deer model applied to Coronation Island in Southeast Alaska, USA. Model was parameterized with values appropriate for wolves and deer (McCullough 1987, Klein 1995, Person et al. 1996). Simulations began with 4 wolves and assumed wolf and deer populations were isolated on Coronation Island. Broken line indicates the actual population estimates for wolves that were introduced to the island in 1960.

packs. Over 95% of radio locations of wolves were at <400 m, which represented the limit of the area normally occupied by wolves. As a result, we divided game management unit 2 into 31 distinct pack areas.

Parameters, r_{max}, C, θ, $S_{t(i)}$, and α were given the same values or distributions used in the simulations of wolves and deer on Coronation Island. Carrying capacity for deer was estimated with habitat capability indices (HCI) for deer associated with each pack area (U. S. Forest Service 1997; Table 22). Indices of habitat capability represented the maximum number of deer that could be supported through a normal winter on a sustained basis in the absence of predation, which coincided with our definition of K. Indices of habitat capability were adjusted by multiplying by 1.09, a conversion factor recommended by Person and Bowyer (1997). Initial deer populations, U_0, for each pack area were arbitrarily set at 75% of K. Values of U_0 were unimportant because the model is insensitive to the level of the initial populations of deer.

Dispersal by wolves between pack areas was allowed with dispersal rate, d, given a normal distribution with a mean of 0.5 and a standard error of 0.3 (Peterson et al. 1984). Annual survivorship of dispersers, s_d, was given a normal distribution with a mean of 0.36 and a standard error of 0.14, which was based on data from our study. Wolf and deer populations in game management unit 2 were considered to be closed to immigration and emigration. Initial number of wolves within a pack area ($P_{0(i)}$) was assigned randomly with a uniform distribution between 0 and 18. The upper bound represented the maximum pack size that we observed (13) divided by 0.71 to account for nonresident wolves.

Table 22. Estimates of carrying capacity (*K*) for deer and length of roads by pack area used in Monte Carlo simulations of the predator-prey model for game management unit 2, which includes Prince of Wales and adjacent islands in Southeast Alaska, USA. Shown are values for 1954 (period prior to initiation of industrial scale logging), 1995 (current levels), and 2045 (50-year projection). All estimates are derived from data provided in the Tongass Land Management Plan revision (USFS 1997), and from Sealaska Regional Native Corporation, and the Alaska Department of Fish and Game, Habitat Division.

	K			Roads		
Pack Area	1954	1995	2045	1954	1995	2045
1	1,985	1,965	1,842	0.0	42.2	87.8
2	3,323	2,339	2,201	0.0	75.6	118.6
3	5,248	5,248	5,248	0.0	0.0	0.0
4	3,274	2,410	2,410	0.0	81.9	82.3
5	3,274	2,410	2,410	0.0	81.9	81.9
6	3,662	1,379	1,379	0.0	181.6	181.6
7	3,525	2,549	2,107	0.0	212.4	339.9
8	2,931	1,583	1,463	0.0	136.2	150.8
9	2,932	2,258	2,138	0.0	68.1	82.6
10	2,932	2,258	2,138	0.0	68.1	82.6
11	3,408	3,408	3,408	0.0	0.0	0.0

12	3,370	3,325	3,195	0.0	11.1	40.6
13	2,826	2,726	2,453	0.0	9.8	84.3
14	2,920	1,856	1,650	0.0	345.8	428.3
15	2,405	1,966	1,866	0.0	75.0	75.0
16	2,923	1,853	1,710	0.0	309.5	367.7
17	2,647	1,304	1,207	0.0	148.4	201.4
18	2,078	840	773	0.0	121.0	142.5
19	3,435	2,092	1,904	0.0	210.3	267.8
20	3,926	1,753	1,618	0.0	305.0	380.0
21	2,450	952	833	0.0	235.3	300.8
22	2,450	952	833	0.0	235.3	300.8
23	3,797	3,067	2,775	0.0	200.5	256.5
24	2,863	2,114	1,384	0.0	217.3	275.8
25	6,684	4,393	3,343	0.0	410.0	601.0
26	3,108	2,419	2,201	0.0	149.2	210.7
27	3,979	2,560	2,296	0.0	332.1	429.1
28	6,619	4,290	4,037	0.0	239.4	328.4
29	2,543	2,088	1,943	0.0	95.9	240.9
30	3,043	2,172	1,886	0.0	240.7	330.2
31	2,228	1,457	1,401	0.0	235.8	260.3
Total	102,788	71,986	66,051	0.0	5,075.4	6,730.2

Human-caused mortality of wolves and deer was included in our model, including effects of roads on rates of mortality from hunting and trapping. We used results from our linear-regression model of wolf harvest versus road length to construct a risk function that predicted effects of roads on harvest of wolves. We calculated the average harvest of wolves for 1990–98 for wildlife analysis areas with no roads (mean = 1.24, SE = 1.17, $n = 7$). The average size of a wildlife analysis area is roughly equivalent to the average size of wolf pack home ranges. Size of packs in autumn averaged about 8 wolves in our study, therefore, we estimated that a wildlife analysis area would contain about 8 resident wolves. Our data indicated that 29% of wolves in an area are likely to be nonresidents. Thus, we estimated total number of wolves in a wildlife analysis area to be 11. An average harvest of 1.24 wolves represented a harvest rate of 11% (1.24/11), which we used as the base harvest rate (t) for wolves. We then divided average harvests for each wildlife analysis area that contained roads by average harvest for wildlife analysis areas with no roads. We regressed these quotients against the lengths of road in wildlife analysis areas that were connected to the main road system in game management unit 2 and again for those that were unconnected. We derived the following risk functions from those regression analyses:

hunting and trapping mortality rate = t [1 + 0.0017 (roads)] for unconnected wildlife analysis areas, and

hunting and trapping mortality rate = t [1 + 0.0057 (roads)] for connected wildlife analysis areas.

Length of roads within a pack area was entered into the appropriate function and the product was then multiplied by $P_{t(i)}$ to estimate number of wolves killed by humans within a pack area. Predictions were given standard errors of 2.1 and 2.7 for areas that are unconnected and connected to the main road system, respectively. Those estimates of uncertainty were based on prediction intervals of the regression functions comparing average harvest and length of road.

We repeated the previous modeling process to estimate effects of roads on harvest of deer. We regressed average deer harvest between 1990 and 1998 against length of roads within wildlife analysis areas connected and unconnected to the main road system in game management unit 2 (Table 23). Average harvest of deer within wildlife analysis areas with no roads was 22.5 (SE = 17.6, n = 7). Person et al. (1996) estimated the deer population on Prince of Wales Island in winter 1995 at 42,000 deer or 6.2 deer/km^2. Average size of a wildlife analysis area is 233 km^2; thus, we estimated that the average deer population in a wildlife analysis area would be about 1,444 deer (233 × 6.2). Dividing average harvest for wildlife analysis areas with no roads by number of deer yielded a crude base rate of deer harvest, h = 0.016 or 1.6%. Using the procedure described for wolves, we produced the following risk functions for deer:

hunting mortality rate = h [1 + 0.010 (roads)] for unconnected wildlife analysis areas, and

hunting mortality rate = h [1 + 0.026 (roads)] for connected wildlife analysis areas.

Length of roads within a pack area was entered into the appropriate function, and the product was then multiplied by $U_{t(i)}$ to predict number of deer killed by hunters within a

Table 23. Results for linear regression[a] of harvest of deer by wildlife analysis area in game management unit 2. Average harvest for a wildlife analysis area between 1990 and 1998 is the dependent variable and length of roads in the area is the independent variable. Results shown are for wildlife analysis areas connected to the main road system on Prince of Wales Island and for those not connected to the main road system. Game management unit 2 includes Prince of Wales and adjacent islands in Southeast Alaska, USA.

Variable	Coefficient	*t*	*P*
Connected			
Constant	20.006	0.517	0.613
Length of Road	0.496	3.492	0.003
Not Connected			
Constant	20.106	2.252	0.044
Length of Road	0.204	2.182	0.050

[a] Regression for connected: $r^2 = 0.45$, $F = 12.19$, $P = 0.003$; for not connected: $r^2 = 0.284$,

$F = 4.76$, $P = 0.05$.

pack area. Standard errors associated with those predictions were 5.4 and 14.6 for areas that were unconnected and connected to the main road system, respectively.

The Tongass Land Management Plan revision (U. S. Forest Service 1997) provided information about current land uses and densities of roads. The plan also included projections of future timber harvest and effects of such harvests on habitat capability for deer, as well as estimates of habitat capability prior to initiation of industrial-scale logging in 1955. We tabulated that information for each pack area to create scenarios for our simulations (Table 22). Projections of road construction were based on a formula of 1.6 km of road for every 2 million board feet (4,723 m^3) of timber harvested (U. S. Forest Service 1997). We devised a pre-logging scenario that represented the conditions prior to 1955, which were held constant during the 90-year period considered in our simulations. We also created a scenario that was consistent with the land-use plan adopted and implemented by the U. S. Forest Service (U. S. Forest Service 1997, Table 22). In that scenario, timber harvest occurs well into the 21st century with approximately 1,700 km of new road construction. The pre-logging scenario served as a "control" for comparing the likely effects of timber harvest and road construction on wolf and deer populations. Monte Carlo techniques were used throughout those simulations and we repeated each scenario 2,000 times.

Under pre-logging conditions, relatively large wolf and deer populations were maintained over the 90 years (Figs. 16 and 17). Average projected population of wolves prior to parturition was 330 (95% C. I. = ± 52) and average deer population was 87,898

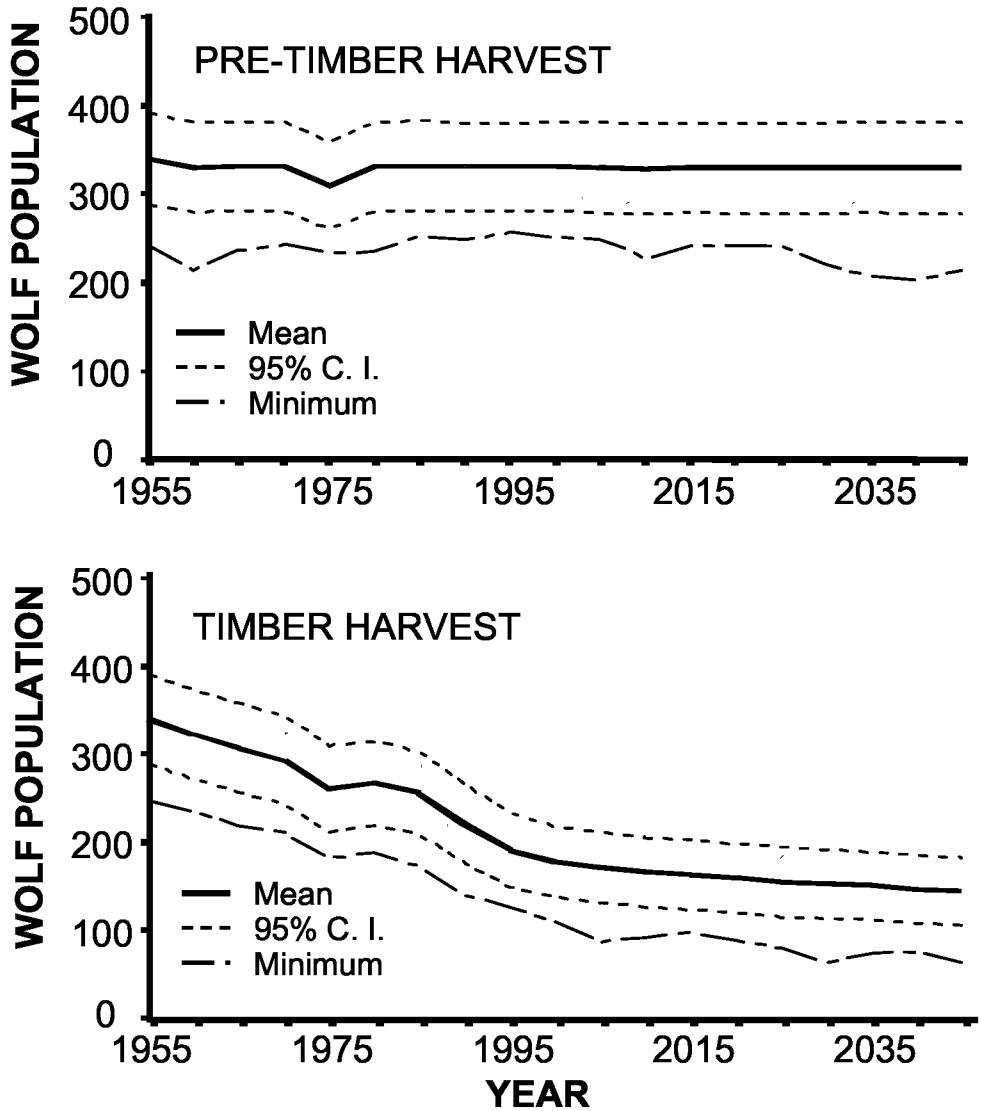

Figure 16. Results of Monte Carlo simulations (n = 2,000) of our wolf-deer model applied to Prince of Wales and adjacent islands in Southeast Alaska, USA. Model was parameterized with values appropriate for wolves and deer. Populations of wolves predicted by our model are shown for a scenario representing conditions that existed prior to industrial-scale logging in 1955 and for a scenario that incorporated past and future effects of timber harvest on K for deer, and effects of road construction on mortality of wolves and deer. Both scenarios included effects of severe winters and harvesting of wolves and deer. The Tongass National Forest Management Plan revision (U. S. Forest Service 1997) was the primary source of data concerning timber harvest, road construction, and K.

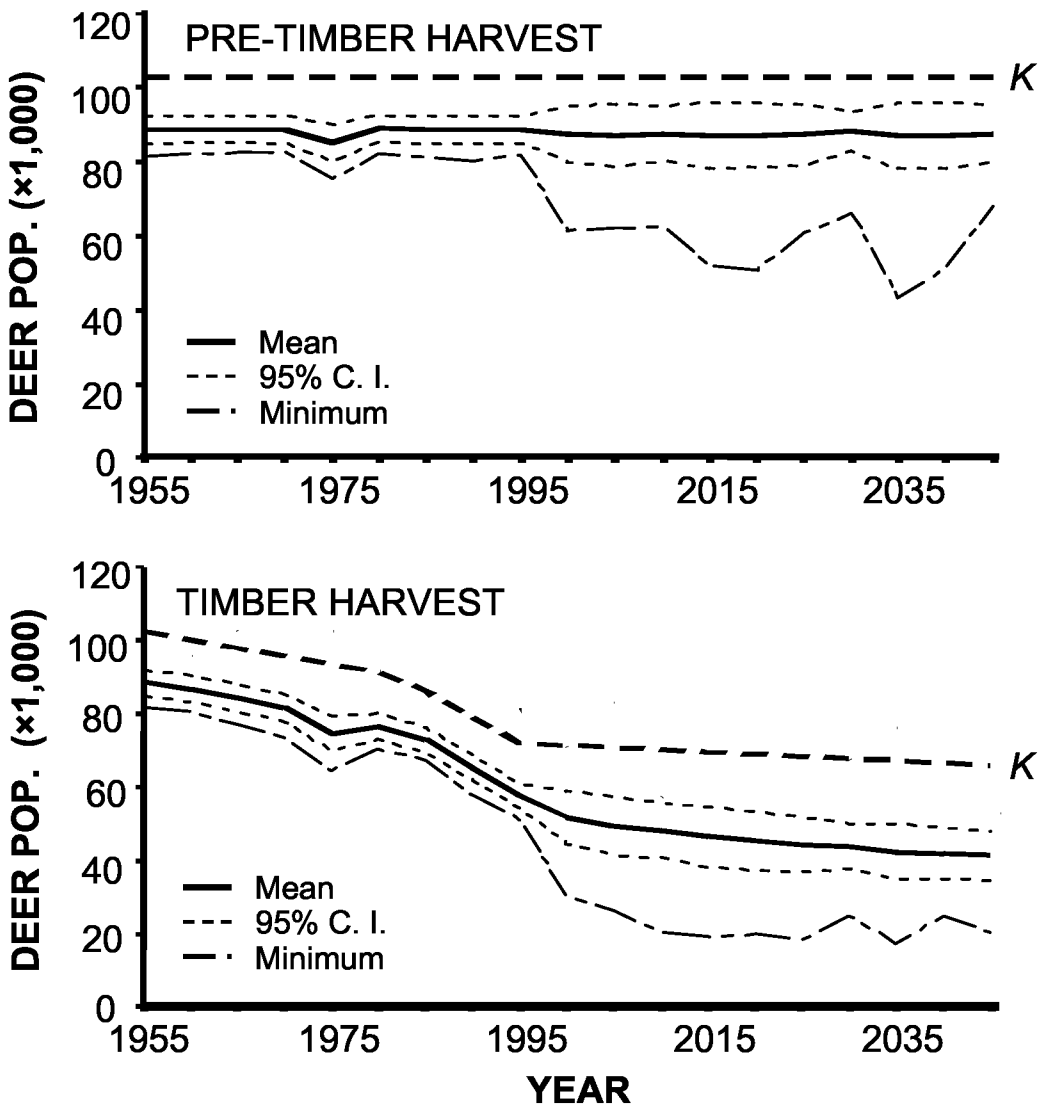

Figure 17. Results of Monte Carlo simulations (n = 2,000) of our wolf-deer model applied to Prince of Wales and adjacent islands in Southeast Alaska, USA. Model was parameterized with values appropriate for wolves and deer. Populations of Sitka black-tailed deer predicted by our model are shown for a scenario representing conditions that existed prior to industrial-scale logging in 1955 and for a scenario that incorporated past and future effects of timber harvest on K for deer, and effects of road construction on mortality of wolves and deer. Both scenarios included effects of severe winters and harvesting of wolves and deer. The Tongass National Forest Management Plan revision (U. S. Forest Service 1997) was the primary source of data concerning timber harvest, road construction, and K.

(95% C. I. = ± 6,134; Fig. 16). The deer population remained stable at about 85% of *K* (Fig. 17). Deer recovered rapidly after severe winters and no simulations showed long-term suppression of deer populations resulting from predation. We arbitrarily considered a population of deer to be suppressed if it remained at a level <50% of *K* for >10 years.

In contrast, simulations incorporating current and future timber harvest predicted that wolf populations declined from a peak of 340 (95% C. I. = ± 52) wolves in 1955 to 192 (95% C. I. = ± 44) in 1995, and projected a further decline to 145 (95% C. I. = ± 38) by 2045 (Fig. 16). The actual wolf population estimate for spring 1995 was 217 (Person et al. 1996), which was close to our projected population of 192 wolves. Deer populations were predicted to decline from 88,583 (95% C. I. = ± 3,612) in 1955 to 57,710 (95% C. I. = ± 3,284) in 1995 and to further decline to 41,339 (95% C. I. = ± 7,154) by 2045 (Fig. 17). Deer were at about 85% of *K* in 1955, whereas by 2045 they are projected to decline to about 63% of *K*. Deer numbers dropped below 50% of *K* at least once in 39% (95% C. I. = ± 1%) of simulations, compared with 0% for pre-logging simulations. In 16% of simulations, deer numbers were suppressed below 50% of *K* for >10 years.

Median number of extant packs predicted in 2045 was 31 (range 26–31) for pre-logging simulations. For simulations incorporating timber harvest, median number of packs in 2045 was 22 (range 12–30). Average percentage of years during the 90-year simulations that a pack area was vacant was 22.5% (95% C.I. = 0–68.5%) for scenarios

with timber harvest and 1.1% (95% C.I. = 0–2.1%) for pre-logging simulations (Table 24). We regressed percentage of years that a pack area was vacant against length of road and *K* for deer in 2045 (Table 25). Results indicated that road length was the most influential factor in our predator-prey model for predicting vacancy by wolves, but *K* for deer also was significant.

The probability of vacancy is a measure of turnover in pack areas. We identified pack areas for which the probabilities of turnover were ≤5%, ≤10%, and >10% owing to the decay of *K* for deer and overharvesting (Fig. 18). Our telemetry data have documented that wolves in 3 of those areas were eliminated by trapping and hunting and subsequently replaced by dispersing wolves (Fig. 18). Areas of high turnover usually are reoccupied by dispersing wolves from neighboring packs, and therefore, function as sinks that rely on other areas as sources.

If Alexander Archipelago wolves had been listed as threatened in 1993 under the Endangered Species Act, harvesting of wolves likely would have been curtailed. We eliminated hunting and trapping of wolves after 1995 in our model and repeated our simulations. For the pre-logging scenario, wolves increased dramatically after 1995 reaching a peak of >600 in 2000 and then declined to a stable population of about 530 wolves (Fig. 19). Median number of occupied pack areas in 2045 was 31 (range = 14–31). The deer population declined 15% after 1995, but remained stable at about 75,000 deer, or 73% of *K*, thereafter (Fig. 20). Deer were resilient to severe winters and suppression of deer populations by predation was rare (<1% of 2,000 simulations). Nonetheless, standard errors for predicted populations of wolves and deer

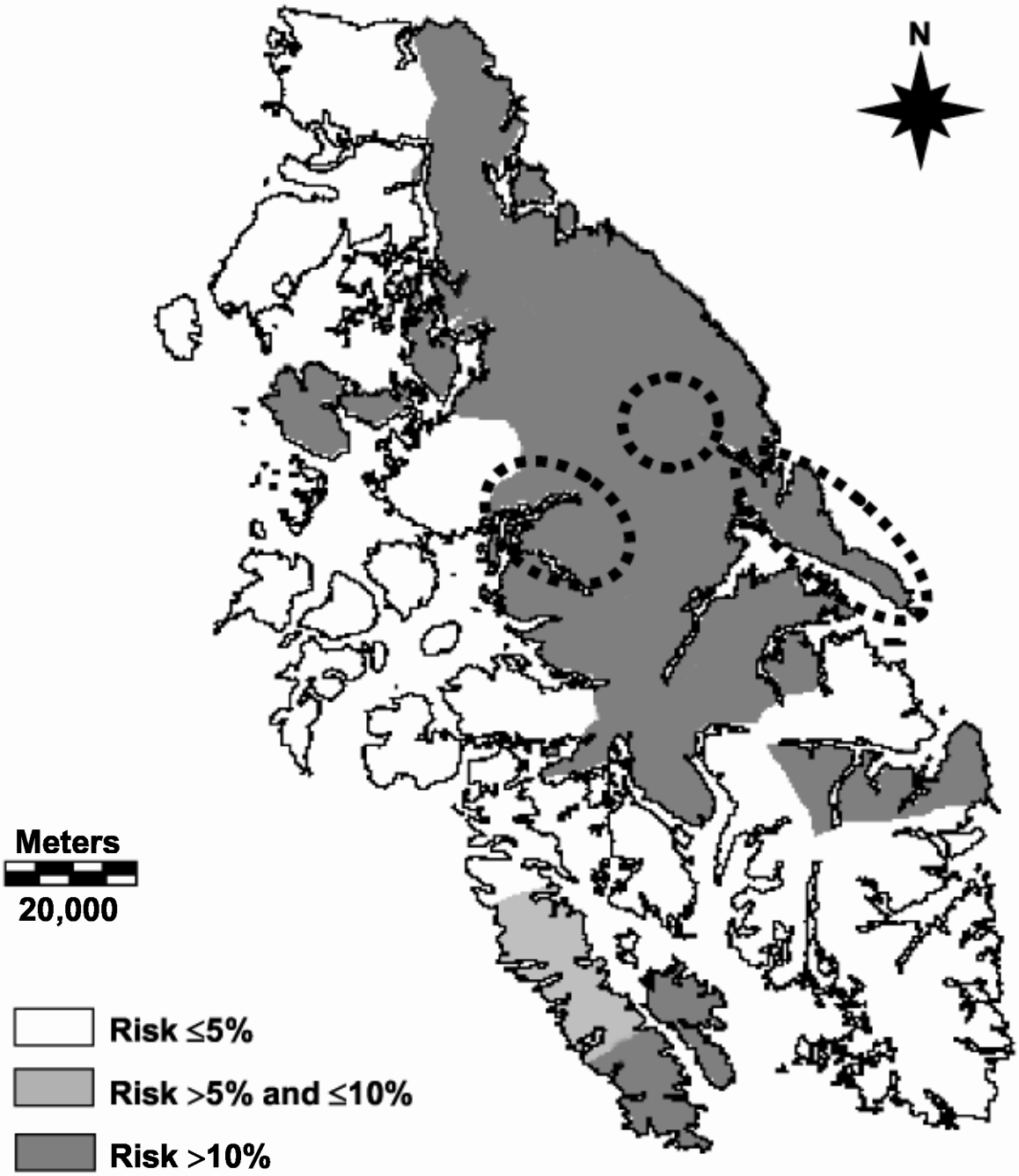

Figure 18. Map of Prince of Wales and adjacent islands in Southeast Alaska, USA, showing the risks of wolf packs being exterminated at least once between 1995 and 2045. Probabilities are based on results of simulations of our wolf-deer model. Areas outlined by dashes are locations where complete turnover of wolves occurred during our study.

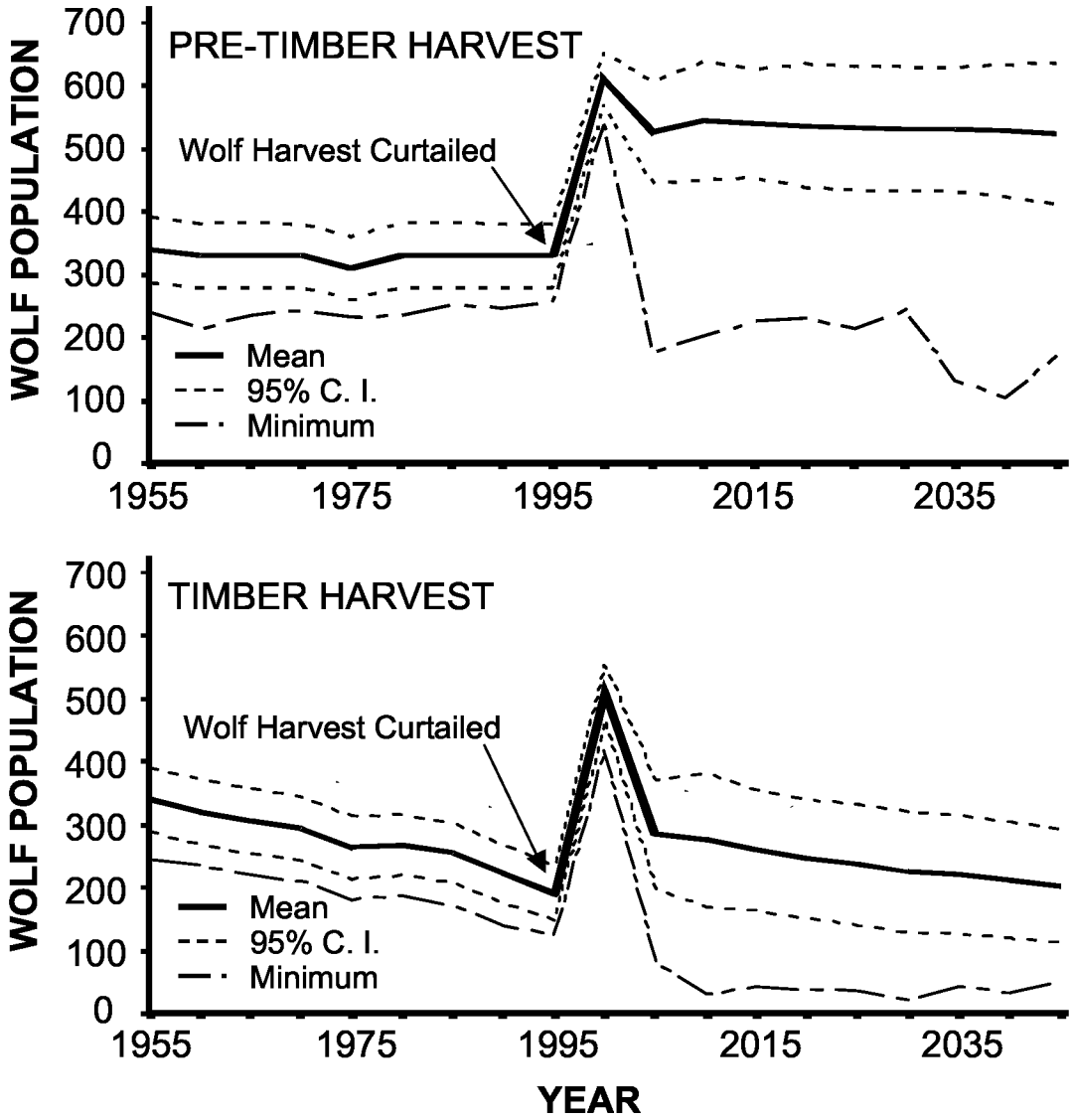

Figure 19. Results of Monte Carlo simulations (n = 2,000) of our wolf-deer model applied to Prince of Wales and adjacent islands in Southeast Alaska, USA. Model was parameterized with values appropriate for wolves and deer. Populations of wolves predicted by our model are shown for a scenario representing conditions that existed prior to industrial-scale logging in 1955 and for a scenario that incorporated past and future effects of timber harvest on K for deer and effects of road construction on mortality of wolves and deer. For both scenarios, harvesting of wolves is curtailed in 1996. Both scenarios included effects of severe winters and harvesting of deer. Harvesting of wolves is included for years prior to 1996. The Tongass National Forest Management Plan revision (U. S. Forest Service 1997) was the primary source of data concerning timber harvest, road construction, and K.

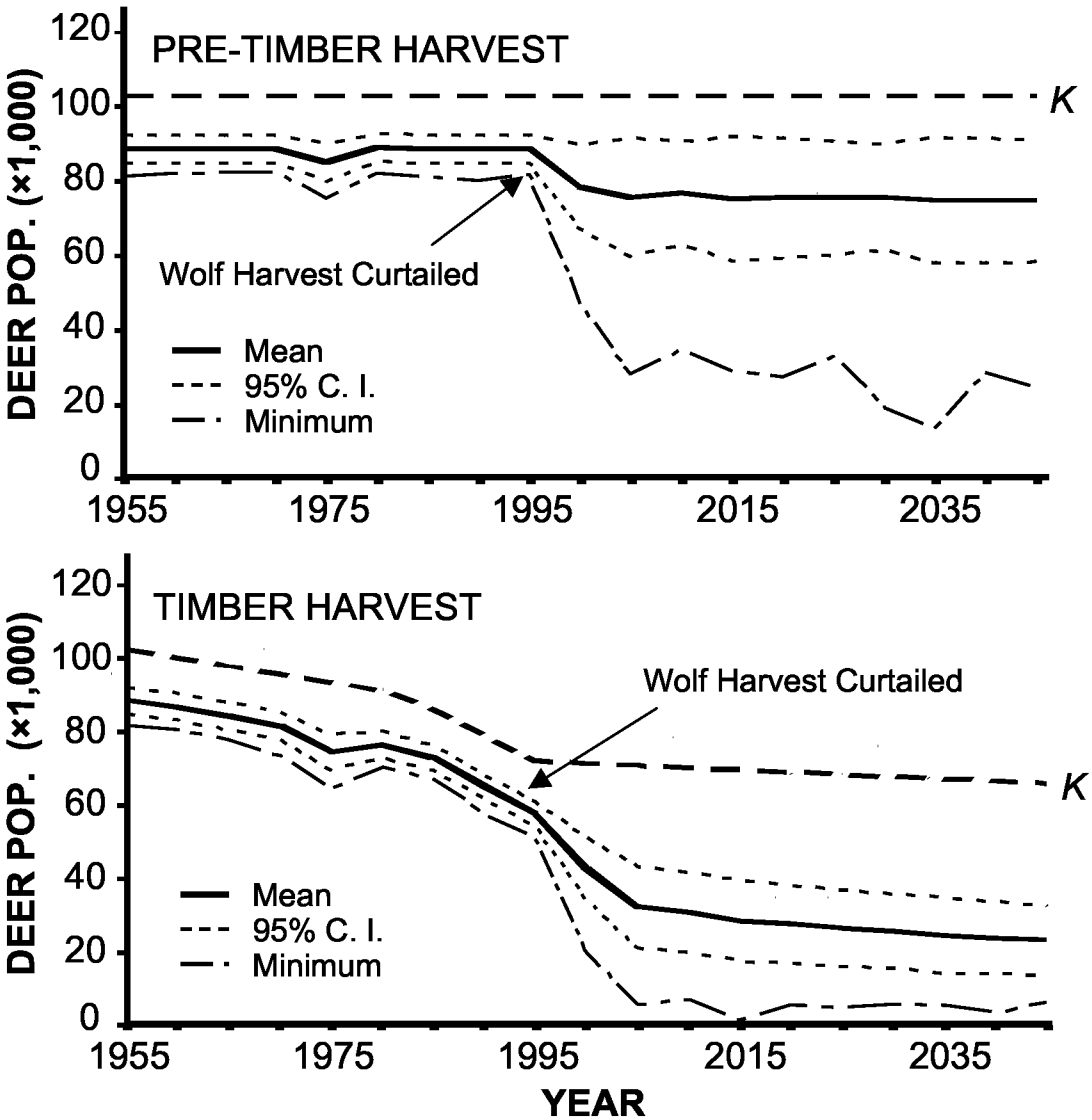

Figure 20. Results of Monte Carlo simulations (n = 2,000) of our wolf-deer model applied to Prince of Wales and adjacent islands in Southeast Alaska, USA. Model was parameterized with values appropriate for wolves and deer. Populations of Sitka black-tailed deer predicted by our model are shown for a scenario representing conditions that existed prior to industrial-scale logging in 1955, and for a scenario that incorporated past and future effects of timber harvest on K for deer and effects of road construction on mortality of wolves and deer. For both scenarios, harvesting of wolves is curtailed in 1996. Both scenarios included effects of severe winters and harvesting of deer. Harvesting of wolves is included for years prior to 1996. The Tongass National Forest Management Plan revision (U. S. Forest Service 1997) was the primary source of data concerning timber harvest, road construction, and K.

Table 24. Results from Monte Carlo simulations (n = 2,000) showing proportion of simulations in which all wolves in a pack area were eliminated at least once during the 90-year period covered by the simulations (1955-2045). Predictions are shown for pre-logging and logging scenarios and are measures of relative turnover of wolves within pack areas. Predictions are for game management unit 2, which includes Prince of Wales and adjacent islands in Southeast Alaska, USA.

Pack Area	Wildlife Analysis Area	Pre-logging % Vacant	Logging % Vacant
1	901	3.1	4.1
2	1332	1.5	2.8
3	902	1.5	2.2
4	1105	1.6	2.6
5	1105	0.7	5.7
6	1105-1106	0.7	23.4
7	1003	0.7	36.5
8	1107	0.7	15.0
9	1107	0.7	4.8
10	1107	0.7	5.0
11	1108	0.7	0.9
12	1209	0.7	1.8
13	1210	0.8	2.9

14	1211	0.7	64.1
15	1212-1213	0.8	2.8
16	1214	0.7	48.9
17	1317	0.7	24.8
18	1315	1.1	58.9
19	1315-1316	0.7	31.3
20	1315-1319-1420	0.7	50.8
21	1318	1.6	56.9
22	1318	0.7	58.7
23	1319-1421	0.7	29.6
24	1319-1421	0.8	32.6
25	1323-1422-1531	0.7	75.2
26	1323-1422-1531	0.7	20.7
27	1323-1422-1531	1.6	4.6
28	1524-1525-1526	1.5	3.7
29	1526-1527-1529	1.5	3.6
30	1527-1528-1529	1.5	4.5
31	1527-1530	1.7	17.3

Table 25. Results of multiple regression[a] of proportion of simulations (n = 2,000) in which a pack area became vacant at least once versus length of roads and carrying capacity for deer (K) projected for the year 2045. Predictions are for game management unit 2, which includes Prince of Wales and adjacent islands in Southeast Alaska, USA.

Variable	Coefficient	t	P
Constant	15.583	1.687	0.103
Length of Road	0.092	4.786	0.000
K	0.007	-2.199	0.036

[a] $r^2 = 0.513$, $F = 16.71$, $P < 0.000$

were more than twice as large as the simulations incorporating harvest of wolves. Further, minimum populations that were predicted for both wolves and deer were substantially lower when wolf harvest was curtailed compared with simulations that allowed harvest. In simulations that included logging, wolf populations increased to a peak of about 500 wolves immediately after harvest was curtailed (Fig. 19). By 2010, populations were reduced to <300 wolves and declined further to about 200 by 2045. Median number of areas occupied by packs was 16 (range = 4–31). Deer populations dropped precipitously after 1995, reaching an average low of 23,300 deer in 2045. As in the pre-logging scenario, variability of populations increased 2 fold from simulations that included harvesting of wolves. The minimum wolf populations were well below 100 animals after 1995, and minimum deer populations were <10,000 deer after 1995 (Fig. 20). In contrast to pre-logging simulations, deer numbers were driven to low levels and populations were much less resilient to severe winters. Deer populations were suppressed at densities <50% of *K* for >10 years in 100% of simulations.

Our simulations of a single, isolated pack area suggested that a minimum carrying capacity of 3,000 deer may be necessary to sustain wolves for a 50-year period (Fig. 21). No levels of *K* achieved 100% sustainability because occasionally conditions unrelated to *K* interacted to eliminate wolves regardless of carrying capacity. We compared those results with estimates of *K* for major islands in game management unit 2 provided in the Tongass Land Management Plan. We predict that only Prince of Wales, Dall, and Kosciusko islands are sufficiently large to support enough deer to sustain wolves in isolation (Table 26). Our predictions are consistent with historical information (Table

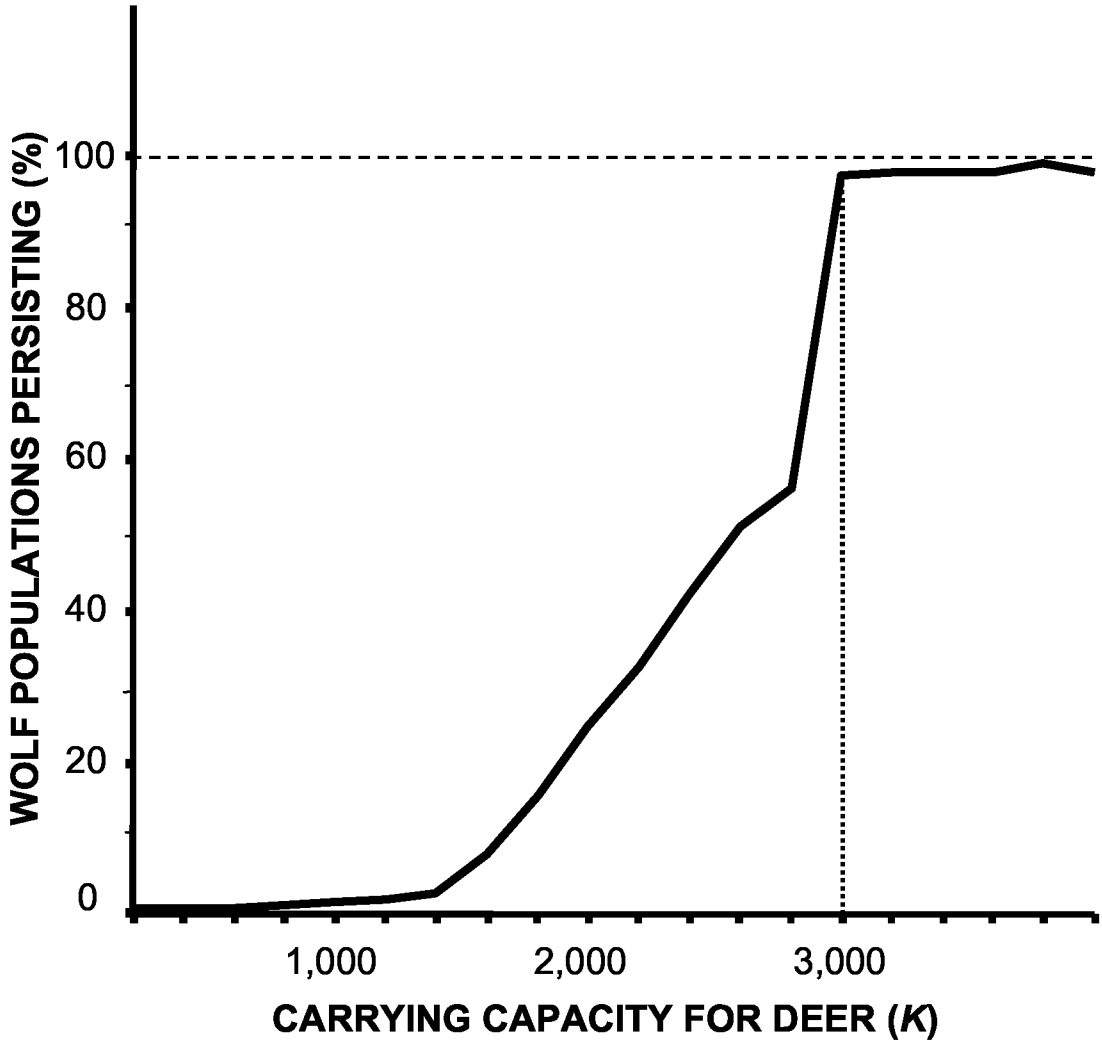

Figure 21. The relation between probability of persistence of a wolf pack over a 50-year period and *K* for Sitka black-tailed deer. The curve reaches an asymptote at approximately 3,000 deer. Results are based on populations of wolves predicted by Monte Carlo simulations (n = 2,000) of our wolf-deer model for a single, isolated wolf-pack area.

Table 26. A list of the major islands in game management unit 2 in Southeast Alaska, USA, indicating the known continuous presence of wolves between 1955 and 2000. Also shown are the sizes of each island and an estimate of the carrying capacity for deer.

Island	Size (Km^2)	K [a]	Wolves
Present [b]			
Prince of Wales	6,361.3	44,433	+
Dall	668.8	5,248	+
Kosciusko	446.6	4,268	+
Sukkwan	180.4	1,284	–
Heceta	177.4	2,573	–
Suemez	150.2	1,965	–
Long	119.1	1,995	–
Baker	116.2	1,411	–
Noyes	97.5	1,183	–
San Fernando	90.3	1,096	–
Coronation [c]	75.5	600	–
Lulu	74.4	903	–
Tuxekan	73.2	1,226	–
Warren	45.8	966	–
Thorne	32.5	203	–
Marble	28.9	483	–

San Juan	21.2	257	–
Orr	20.3	340	–

[a] Carrying capacity is based on deer habitat capability estimates (USFS 1997) adjusted by multiplying by 1.09.

[b] Presence of wolves is based on interviews with Alaska natives, trappers, fishers, biologists, and harvest records.

[c] Coronation Island is not included in GMU 2 but is listed for comparison. *K* is based on the maximum number of deer estimated to be on the island prior to the introduction of wolves in 1960 (Klein 1995).

26). Small groups of islands such as the Baker-Lulu-Noyes group may have supported wolves continuously, at least since 1955. Nonetheless, individually those islands are too small. Historical presence or absence of wolves on some islands may have been affected by hunting and trapping rather than number of deer available. Indeed, in 1995 and again in 2000, a single trapper almost eliminated wolves on Heceta Island. Nevertheless, this only serves to emphasize that islands or patches may need to be larger and of higher quality than our predictions indicate to enable wolves to persist in the presence of determined exploitation. Our results indicated that only wolves on the 3 largest islands in game management unit 2 are likely to function as source populations in the region.

DISCUSSION

Wolf Ecology

Composite home ranges of wolf packs in our study were similar to MCP home ranges previously reported for wolves on nearby Revillagigedo Island ($\bar{x}$ = 279 km^2, range = 79–47 km^2) by Smith et al. (1987). Home ranges, however, were considerably smaller than those reported for wolves in other parts of Alaska, even though average size of packs was similar. For example, home ranges of wolf packs in south-central Alaska, Kenai Peninsula, and Denali National Park were 1,645 km^2, 638 km^2, and 1,330 km^2, respectively (Ballard et al. 1987, Peterson et al. 1984, Mech et al. 1998). Wolves in those areas primarily preyed on moose and caribou (*Rangifer tarandus*), whereas wolves in Southeast Alaska mostly preyed on Sitka black-tailed deer.

Our estimates of home range generally were larger than home ranges reported for wolves in other areas with similar average sizes of packs where white-tailed deer (*O. virginianus*) were their principal prey. For example, home ranges of wolf packs in 4 studies in northern Minnesota were 110, 116, 192, and 243 km^2 (Van Ballenberghe et al. 1975, Fuller 1989, Berg and Kuehn 1982, Mech 1973). Similarly, 2 studies conducted in east-central Ontario and a study in southern Quebec reported home ranges of 175, 224, and 199 km^2, respectively (Pimlott et al. 1969, Kolenosky 1972, Potvin 1988). Fuller (1989) documented a strong negative relation between density of deer and size of home ranges of wolf packs. Home ranges for wolf packs in our study were similar to those reported by Fuller for wolves in areas where deer were at densities <4 deer/ km^2 (Kolenosky 1972, Mech 1973, Potvin 1988), indicating that density of deer may have been low in our study area. Nevertheless, Person et al. (1996) estimated a density of 14.6 deer/ km^2 on winter range on Prince of Wales Island or an overall density of 6 deer/ km^2. Perhaps susceptibility of deer to predation rather than density of deer influenced home-range size. Deer occupying logged habitats may be unavailable to wolves during snow-free months if the slash and debris left after logging hinders ability of wolves to hunt. This notion is supported by wolves in the Honker Divide and Thorne River packs having the smallest home-range indices of 7 packs studied (Table 16); home ranges of both packs encompassed the least amount of logged habitat. Conversely, Ratz Harbor and Steelhead Creek packs had the largest home-range indices (Table 16), and logged habitat constituted large proportions of their home ranges. Wolves generally selected for closed-canopy and open-canopy old-growth forest, while avoiding or showing

neutral selection for clearcuts and seral forests. Further, analysis of feces from wolves in our study indicated that percent occurrence of deer remains in feces was lower for wolves occupying logged landscapes than for wolves inhabiting unlogged areas (Kohira and Rexstad 1997).

A positive correlation between pack size and home-range size has been noted by several researchers (Peterson et al. 1984, Ballard et al. 1987, Fuller 1989). Mech et al. (1998), however, suggested that this relation was primarily a phenomena associated with exploited wolf populations. The strong correlation of pack size and home range that we observed in wolves in Southeast Alaska contributes little to resolving that issue because those wolves were exposed to intense exploitation. Our study is the first, however, to describe a positive correlation between pack size and critical habitat for ungulate prey. In addition, we provided evidence of a negative correlation between home-range size of wolf packs and critical habitat for deer. We also observed wolf packs located in areas where deep snow accumulated select closed-canopy old-growth forests in winter. Conversely, packs occupying areas with little snow accumulation did not select closed-canopy old-growth forests in that season. That pattern of habitat selection likely was driven by the short-term availability of deer and, therefore, was influenced by ephemeral phenomena such as winter weather. In contrast, the relation between pack size, home range, and winter habitat for deer probably was indicative of a longer-term influence of habitat on density of deer.

We observed that home ranges during pup-rearing season were much smaller than home ranges in autumn and winter. That pattern was consistent for all packs that were

monitored during both seasons. Wolf packs with pups tended to remain near denning and rendezvous areas between May and mid-August. A similar pattern was reported by Mech et al. (1998) for wolves in Denali National Park, Alaska. Other studies, however, concluded that home ranges of wolf packs did not differ between summer and winter (Van Ballenberghe et al. 1975, Fritts and Mech 1981, Fuller 1989, Potvin 1988). Annual composite home ranges for wolf packs reported by Fuller (1989) and Van Ballenberghe et al. (1975) for wolves in Minnesota were similar to pup-rearing home ranges for packs in our study. Van Ballenberghe et al. (1975) noted that wolves concentrated activity near large wintering areas (i.e., yards) for white-tailed deer, and therefore, wolf packs in their study area ranged over relatively small areas in winter. Winter habitat for Sitka black-tailed deer was broadly distributed in small patches within our study area. Consequently, small concentrations of deer were widely distributed in winter, forcing wolves to maintain relatively large winter home ranges to encompass sufficient prey. Smaller home ranges during the pup-rearing season ostensibly resulted from reduced mobility of pups (Mech et al. 1998).

Our radio telemetry data indicated that wolves selected habitat at low elevations during all seasons. In winter, deer concentrated in habitats at low elevations as snow accumulated at high elevations, and wolves probably concentrated most of their activity where deer were available. A large portion (75%) of a deer population migrates to high elevations during summer to forage on high-quality forbs and shrubs that are abundant in alpine habitat (Schoen and Kirchhoff 1985, McNay and Voller 1995). Wolves probably do not follow migratory deer because they are constrained by the needs and

mobility of pups. Thus, migratory deer likely reduce their risk of predation during summer because wolves remain mostly at low elevations. Seasonal movements to elevations above those typically frequented by wolves and bears have been observed in other ungulates, ostensibly to avoid predators (Barten et al. 2001). Nonmigratory deer may suffer rates of predation higher than migratory deer. Indeed, on Vancouver Island, British Columbia, McNay and Voller (1995) indicated that annual survivorship of migratory deer was 90% compared with 77% survivorship for nonmigratory deer, with most mortality resulting from predation. Likewise, during a normal winter, resident mule deer experienced higher mortality from predation than did migrants in montane southern California (Nicholson et al. 1997). Deer that remain at low elevation during summer and early autumn also are most accessible to hunters, and may be vulnerable to mortality from a combination of hunting and predation. Consequently, the perception of humans hunting deer at low elevations may be that wolves are depleting deer, even though deer are abundant at higher elevations.

A large proportion of wolves we radiocollared dispersed or exhibited extraterritorial behavior. We could not determine if extraterritorial wolves were related to resident packs that they orbited. Those wolves may have been pack members that were searching for vacant areas and reproductive opportunities near home ranges of their natal packs, or they may have been unrelated animals that had terminated dispersal behavior and were attempting to settle by joining a resident pack or seeking vacant habitat between resident packs.

Low densities of prey may induce dispersal and extraterritorial behavior in wolves (Peterson and Page 1988, Fuller 1989, Gese and Mech 1991). Dispersal, however, was not likely stimulated by low densities of prey in our study area. Deer were moderately abundant throughout our study, although availability of deer to wolves may have been restricted in logged areas. In addition, supplemental prey such as beaver and salmon were seasonally available (Kohira and Rexstad 1997, Person et al. 1996). None of the wolves that we radiocollared showed evidence of food stress.

Fritts and Mech (1981) suggested that dispersal may be induced if vacant territories exist. Those authors concluded that dispersal was a mechanism by which wolves rapidly colonize unoccupied areas. Reproductive opportunities afforded by vacant territories may stimulate dispersal in wolves of breeding age. In our study, intensive harvest of wolves created vacant territories that were rapidly colonized by wolves dispersing from nearby packs. In wolf populations where mortality is high, dispersing and extraterritorial wolves may be more successful in finding vacant territories in which to settle, or in being accepted into other established packs (Fritts and Mech 1981, Ballard et al. 1987). We suspect that intensive harvest of wolves within our study area created vacant territories and induced some dispersal that we observed.

We believe that dispersal of wolves to and from game management unit 2 and the mainland, or other major island groups, was restricted. All wolves that dispersed in our study stayed on Prince of Wales or nearby islands. We believe dispersal to or away from Prince of Wales and adjacent islands is rare and unlikely to have much effect on wolf population dynamics. Consequently, wolves in game management unit 2 probably

are a subpopulation within a larger patch-structured population of wolves in Southeast Alaska (Taylor 1990). Movement between subpopulations may be sufficient for genetic interchange (Shields 1995), but insufficient to have much effect on the population dynamics of subpopulations. Movement of wolves between islands within game management unit 2 was common with ocean swims ranging from 0.1 km to 4 km. Our results indicate that wolves on Prince of Wales and nearby islands were a single breeding population during our study.

Hunting and trapping were dominant sources of wolf mortality in our study. In heavily exploited populations, mortality from natural causes (e.g., starvation, accidents, disease, and fighting) is small, typically averaging 5–10 % per year (Fuller 1989). Results from our study were consistent with those findings. Many aspects of wolf ecology that we studied including home-range size, pack size, dispersal, temporal patterns of activity, and habitat selection could be linked to human disturbance. We already have noted potential effects of human disturbance on home-range size and dispersal. In addition, we observed that wolves were more active at night, and used roads and logged habitat more at night than during daytime. Wolves may have behaved this way to avoid encounters with humans. Kitchen et al. (2000) demonstrated that coyotes (*Canis latrans*) were active mostly at night during periods of intense persecution by humans. After the persecution stopped, coyotes switched to diurnal patterns of activity. Unfortunately, no other studies of wolves contain information on nocturnal activities or effects of human disturbance with which to compare our results.

Studies in Wisconsin, Michigan, Ontario, and Minnesota indicated a strong relation between road density and presence or absence of wolves (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989). Those studies documented that wolves generally failed to survive in areas with road densities >0.6 km/km^2, whereas wolves persisted in similar areas with lower densities of roads. Several plausible explanations for the absence of wolves in densely roaded areas exist. In some instances, wolves may avoid roaded areas depending on the type of human use roads receive (Thurber et al. 1994). In most instances, the absence of wolves was a direct result of mortality associated with roads (Van Ballenberghe et al. 1975, Mech 1989, Berg and Kuehn 1982). Substantial human-caused mortality can occur even when wolves are completely protected from hunting and trapping (Fritts and Mech 1981, Fuller 1989). Fuller (1989) reported that 80% of identified mortality in a protected study area was caused by people. Similarly, Mech (1989) noted that 60% of mortality in a roaded study area was human caused, whereas no mortality was human caused in an adjacent roadless area.

Citing the expansion of wolf populations in Minnesota, Wisconsin, and Michigan, Mech (1995) suggested that road density was not really a deterrent, provided human populations were tolerant of wolves. Nevertheless, in an analysis of habitat selection by colonizing wolves, Mladenoff et al. (1995) reported that roadless areas were preferred, and occupation of roaded landscapes occurred when few roadless areas remained. In all circumstances in which wolves successfully inhabited roaded or developed areas, adjacent roadless areas were present.

Person et al. (1996) noted that mortality of wolves from hunting and trapping was significantly related to linear kilometers and density of roads within wildlife analysis areas on Prince of Wales and nearby islands. Our results reinforce those findings. We observed wolves occupying areas with densities of roads greatly exceeding 0.6 km/km^2. Nonetheless, roads had a profound effect on mortality of wolves from hunting and trapping and that effect was significant, even in areas where roads were not easily accessible to motorized traffic.

Predator-prey Modeling

Our simulations predicted that the wolf population in game management unit 2 likely will decline, perhaps as much as 25%, between 1995 and 2045 as a result of the combined effects of past timber harvest and future forest management described in the revised Tongass Land Management Plan (U. S. Forest Service 1997). The population of wolves could be reduced by 2045 to a level <50% of what may have existed prior to initiation of industrial-scale logging in 1955. Despite a decline, our simulations indicated that there is little risk that wolves will become extinct on Prince of Wales and adjacent islands in the next 40–50 years. We emphasize that contingencies such as future changes in management plans, regulations for deer and wolf harvest, human population, and climate all may influence wolf and deer populations in ways unanticipated by our simulations. For example, declining populations of deer may stimulate sport and subsistence hunters to demand wolf control in game management unit 2. Should that happen, our estimates of the risk of extinction of wolves may be optimistic. In contrast, global warming (Intergovernmental Panel on Climate Change

1996) may reduce the frequency of severe winters and reduce the risk of steep declines in deer population. Nevertheless, models cannot accommodate all contingencies without becoming intractable and losing focus (Hilborn and Mangel 1997).

Logging and road development have facilitated human access and resulted in periodic extirpation of wolves from some wildlife analysis areas in game management unit 2. Predictions from our simulations highlight areas in game management unit 2 within which wolves likely will experience unsustainable mortality from human causes. Those areas may become population sinks for wolves. Historical data concerning the continuous presence or absence of wolves on islands in unit 2, and results from our simulations, suggest to us that only Prince of Wales, Kosciusko, and Dall islands are large enough to permanently sustain wolves. Thus, the wolf population in game management unit 2 probably is characterized by a source-sink structure (Pulliam 1988, Howe et al. 1991), in which the 3 largest islands support the source population. Smaller islands nearby probably are too small to permanently sustain wolves, and thus, function as sinks that periodically draw dispersers from sources. Timber harvest complicates population structure further by reducing the extent of habitat that can sustain a source population of wolves and by creating new population sinks.

Forest-management practices on Prince of Wales and nearby islands will reduce *K* for deer 8% over the next 40–50 years, and 36% from what it was prior to initiation of industrial-scale logging in 1955 (U. S. Forest Service 1997). We predict that the population of deer will decline 28% between 1995 and 2045, and possibly as much as 63% from what it was in 1955. Our predictions indicate that deer will decline

disproportionately to the decay of *K*. Thus, a small change in *K* may precipitate a large change in deer numbers; an outcome also predicted by McCullough (1979) for populations of white-tailed deer. That outcome from our model stems from the nonlinear density-dependent relation between annual recruitment to populations of deer and density of deer with respect to *K*. The area under the curve representing maximum sustained yield declines in a negative-exponential fashion as *K* is reduced (Fig. 22). Consequently, net annual recruitment of deer, which represents the portion of a deer population that can be removed by predators and hunters without causing a decline in the population, is reduced disproportionately to the decline in *K*. As *K* decays, wolves and other predators such as black bears will have a greater effect on deer numbers. Indeed, our simulations agree with those of Van Ballenberghe and Hanley (1984) and indicate that long periods in which populations of deer are suppressed by predation likely will be common in the future.

Our simulations suggest that dynamics of the wolf-deer system in game management unit 2 will become volatile and that variability in the system will be increased if wolves are not hunted or trapped. The base rate of harvest used in the model is a percentage of the wolf population, and therefore, harvest tends to be in synchrony with the population, dampening fluctuations. We acknowledge, that if harvesting of wolves is asynchronous with the population, fluctuations in wolf population likely would be exacerbated rather than dampened. Nevertheless, current harvest regulations for game management unit 2 restrict legal killing of wolves to 30% of the estimated population (Alaska Department of Fish and Game 2001); thus, actual

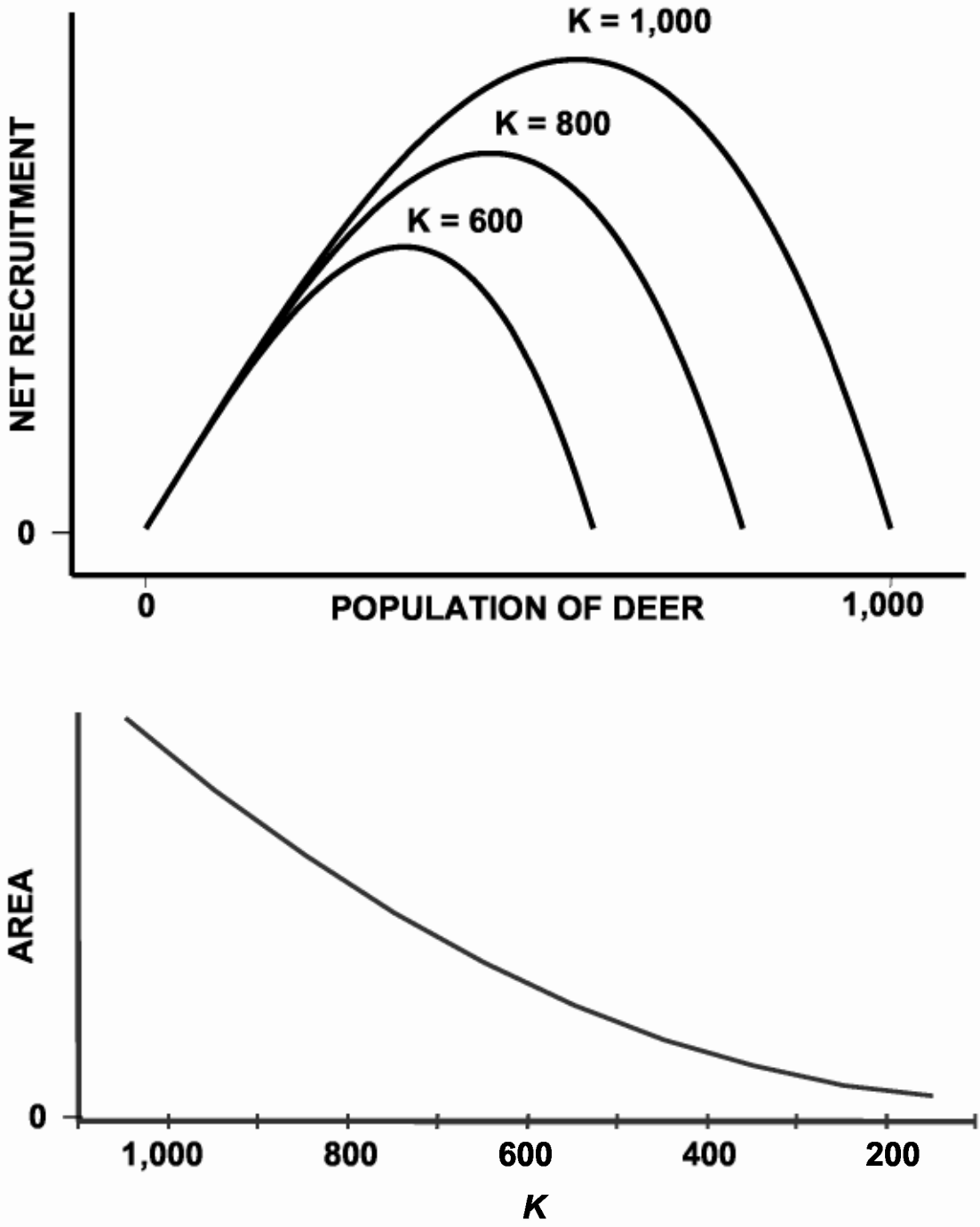

Figure 22. Upper graph shows hypothetical recruitment or maximum sustained yield curves for Sitka black-tailed deer for different levels of *K*. Lower graph indicates relation between *K* and area under the recruitment cure. As *K* is reduced, the area under the recruitment curve declines in a nonlinear fashion.

harvest theoretically should track the population as in our model. We suggest that prior to industrial-scale timber harvesting, productivity of the deer population likely compensated for effects of wolf predation regardless of whether wolves were harvested. Harvesting of timber has degraded the productivity of the habitat for deer by reducing *K*, and creating conditions that increased effects of predation on deer populations. Thus, harvesting of wolves may be necessary to avoid sustained suppression of populations of deer particularly after severe winters (Hatter and Janz 1994).

Numerous studies have focused on effects of wolf predation on ungulate populations and concluded that predation was the dominant factor controlling the behavior of the system (Gasaway et al. 1983, Gasaway et al. 1992, Messier 1994). Those "top down" studies tend to minimize the "bottom up" effects of *K* for ungulates on predator-prey dynamics. Our work emphasizes the importance of *K* for ungulate prey as a factor influencing the behavior of wolf-ungulate systems. Our model generally behaves as a ratio-dependent predator-prey system (Berryman 1992, Ginzburg and Ak÷akaya 1992). For example, reduction in *K* for deer results in declines of both deer and wolves. Nonetheless, as *K* declines, stochastic events, such as severe winter weather, and time lags in the numerical response of wolves to changes in the density of deer, may combine to temporarily limit the number of deer to low levels without a concurrent reduction in wolves. Under those circumstances, it may appear temporarily that "top down control imposed by predation may supersede effects of *K* on deer; an interpretation that could lead resource managers to undervalue habitat. For example, researchers studying wolves and deer on Vancouver Island, Canada, suggested that

declines in populations of deer were the result of predation by wolves, and that changes in habitat due to logging had little effect on numbers of deer (Atkinson and Janz 1994, Hatter and Janz 1994). Winter weather was mild during that study and relations between deer and habitat were not examined. The authors indicated that numbers of deer declined in logged and unlogged landscapes, and thus, habitat change was not a factor influencing the decline of deer population. No information concerning relative densities of deer in logged and unlogged landscapes was provided. The authors suggested that when numbers of deer were kept low by predation, it was difficult to justify deferring the logging of winter habitat for deer. In our view, studies such as those on Vancouver Island simply demonstrate that densities of ungulates are lower when exposed to predation by wolves than when wolves are absent. We suggest that the potential for populations of deer to rebound from low levels imposed by weather and predation is as dependent on *K* as it is on the reduction of predators. Indeed, using low densities of deer to justify reducing *K* for deer simply perpetuates the problem. Our simulations indicate that longer and more frequent periods in which numbers of deer are kept at low levels by predation likely would result from a decline in *K*. For Alexander Archipelago wolves in Southeast Alaska, human activity is altering habitat for deer that will likely result in a long-term and permanent decline of *K* for deer. We believe all facets of the

predator-prey system will be immured within boundaries set by that change.

Management Implications

We documented the demise of packs from hunting and trapping that was facilitated by human access along roads. Although we agree that wolves are not averse to using roads, we are not as confident as Mech (1995) about managing human-caused mortality of wolves, particularly in Southeast Alaska. Roads facilitated legal and illegal harvest of wolves during our study and enforcing trapping and hunting regulations was difficult because of island topography and vastness of the region. Harvesting of wolves under current conditions in Southeast Alaska likely does not threaten wolves with extinction, even in areas such as Prince of Wales Island. Indeed, harvesting of wolves may serve to dampen fluctuations in wolf and deer populations, particularly following severe winters. Nonetheless, as *K* declines, deer populations will be less resilient to predation by wolves and hunting by humans. Conflict between humans and wolves over deer likely will intensify and wildlife managers will be faced with the dilemma of satisfying the demands of human subsistence users and simultaneously protecting the viability of wolf populations. Under those circumstances, human-caused mortality of wolves may be difficult to manage. We believe that managing human access by closing roads for motorized use and limiting construction of new roads are measures necessary to conserve wolves over the long term. Managing human use of existing Forest Service roads is difficult and local opposition often prevents land managers from implementing plans affecting use of roads. Limiting construction of new roads would be a more effective strategy.

Wolves and deer in game management unit 2 are subject to "succession debt," a term analagous to "extinction debt" (Tilman et al. 1994), wherein, the inexorable pattern of forest succession initiated by past harvesting of timber will have long-term effects on the predator-prey system. Current healthy populations of wolves and deer are misleading indicators of future conditions as *K* for deer declines. Future changes in forest management likely will do little to alter the decline in habitat for deer because most of that loss will be due to logging that occurred prior to the revision of the Tongass Land Management Plan in 1997 (U. S. Forest Service 1997). In addition, our simulations indicate that the population of wolves after 2045 may be close to the minimum population of 100 wolves recommended by the U. S. Fish and Wildlife Service for a subpopulation within a larger structured or metapopulation of wolves (Fritts 1994). The population of wolves in game management unit 2 will be close to a marginal level, limiting options for population management, and making it more vulnerable to stochastic events that effect mortality of wolves and deer.

One of the most important measures for the conservation of wolves in Southeast Alaska is to maintain abundant high-quality habitat for Sitka black-tailed deer. The U. S. Forest Service employs a simple habitat-suitability model to evaluate effects of timber-harvest plans on deer (Suring et al. 1993). The model is an important part of the analysis used in environmental impact statements mandated by the National Environmental Policy Act (NEPA) for any plans allowing substantial timber harvest within the Tongass National Forest. The original intent of modeling habitat capability for Sitka black-tailed deer was to provide an index, representing the potential of a

habitat to support deer, to be used to compare effects of alternative plans for timber harvest on deer. Nonetheless, under the Alaska National Interest Lands Conservation Act (ANILCA), the U. S. Forest Service is mandated to maintain populations of deer sufficient for the needs of subsistence hunters. Consequently, biologists from the U. S. Forest Service regularly use the habitat-capability model as an analog for actual numbers of deer to compare effects of alternative timber harvest plans on the supply of deer to subsistence users (U. S. Forest Service 1997). To use the model for that purpose, an assumption of a linear relation between changes in habitat suitability and deer populations is necessary. Our work challenges that assumption and suggests changes in productivity of habitats to support deer will have disproportionate effects on deer populations where predation by wolves is a factor. We emphasize the need to examine the effects of timber harvest, or any other disturbance to the system, at the community level rather than for only individual species. Modeling the wolf-deer system, as we have done, is better suited for assessing effects of forest management on deer populations than simple habitat-suitability models.

The viability of small, disjunct populations of wolves is contingent on their valuation by humans and the sustained availability of ungulate prey. In an analysis of habitat for wolves colonizing northern Wisconsin and Michigan, Mladenoff et al. (1995) concluded that density of roads and human population were main determinants of habitat selection by newly established wolves. They indicated that density of deer in an area was not a significant predictor of occupancy by wolves. Nonetheless, Mladenoff et al. (1995) acknowledged that density of deer in their study area was positively correlated

with areas of human activity, a relation in contrast to our study area. Mladenoff et al. (1995) reported that wolves avoided areas of human activity, and thus, the correlation between density of deer and wolf activity may have been obscured. Our model simulations suggest that density of prey is an important factor influencing the long-term viability of small, insular populations of wolves. Home-range size, density of wolves, resiliency of wolves to natural or human-related mortality, and avoidance of conflicts with hunters, are all contingent on the availability of ungulate prey. Indeed, we documented wolves exploiting landscapes that were heavily modified by human activity, and which exposed them to high rates of mortality. Our simulations indicate that persistence of wolves under those circumstances requires management of human-related causes of mortality, and maintaining high-quality habitat for ungulate prey. Those considerations are more important for small, insular populations of wolves that are constrained spatially, and are not buffered by immigration. Habitats within landscapes change over time because of natural and human-caused processes, and areas that are reserved for the conservation of wolves should encompass sufficient habitat for ungulate prey to allow for a shifting mosaic of habitat quality. Consequently, areas set aside for the conservation of wolves may need to be much larger than would be suggested by current conditions. A dynamic model of habitat change linked to a spatially dependent model of predator-prey dynamics, as we have done, should provide a useful tool to evaluate the adequacy of reserves and to better anticipate the long-term consequences for wolves of habitat change.

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