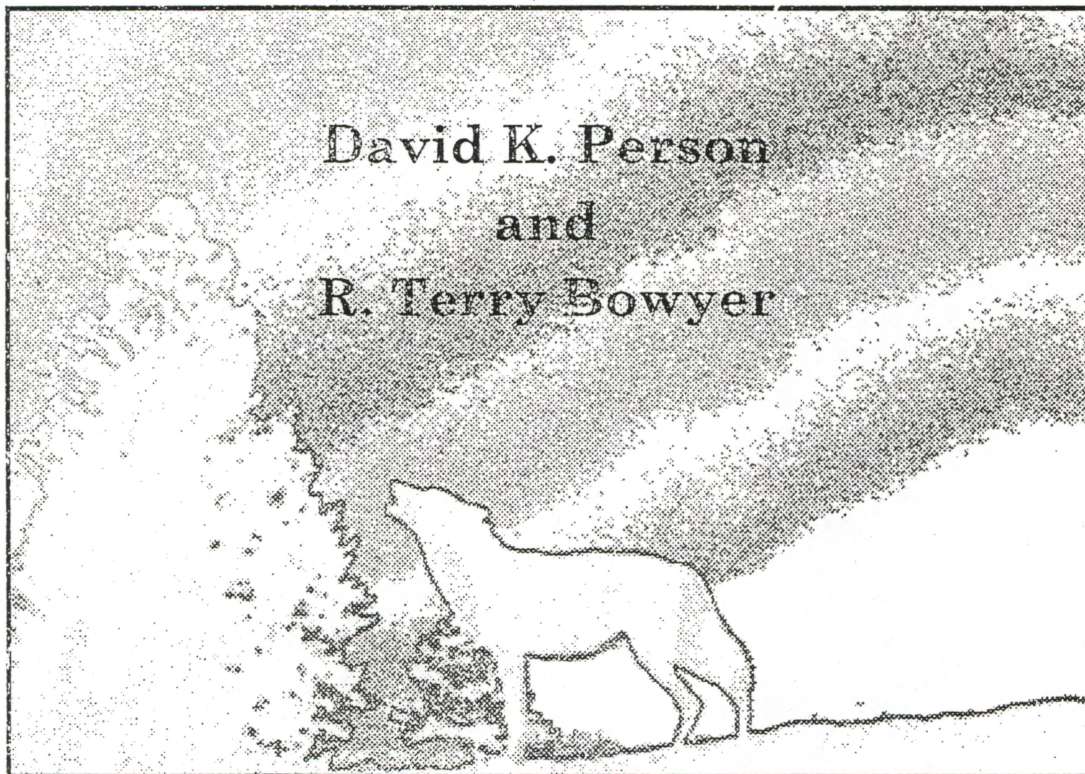


**Population Viability Analysis
of Wolves on Prince of Wales
and Kosciusko Islands,
Alaska**

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and
R. Terry Bowyer



**POPULATION VIABILITY ANALYSIS OF WOLVES ON
PRINCE OF WALES AND KOSCIUSKO ISLANDS,
ALASKA**

**Final Report to the
U. S. Fish and Wildlife Service**

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INTRODUCTION

The Alexander Archipelago wolf (*Canis lupus ligoni*) is a relatively small wolf that occupies most of the islands and the narrow strip of mainland that constitute southeastern Alaska (Figure 1). Most of its range lies within the Tongass National Forest, the largest National Forest in the United States. The wolf population in southeastern Alaska probably numbers about 1,000 animals but may be subdivided into smaller subpopulations by the island topography of the region (Person et al. 1996). The viability of small wolf populations, such as those that exist on some of the islands of southeastern Alaska, is of general concern to biologists that are involved with the reintroduction of wolves to appropriate public lands. These efforts usually involve the conservation of small, relatively isolated wolf populations (Fritts et al. 1995, Parsons and Nicholopoulos 1995, Phillips et al. 1995). The islands of southeastern Alaska may provide an extensive natural laboratory in which to study the effects of isolation, island or patch size, and human disturbance on small wolf populations.

The landscape in the southern portion of the Alexander Archipelago has undergone rapid change due to extensive timber harvesting, resulting in the loss of highly productive old-growth forest stands that are important winter habitat for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) (Wallmo and Schoen 1980, Schoen and Kirchhoff 1985, Kirchhoff and Schoen 1987, Hanley 1984, 1987, and Schoen and Kirchhoff 1990). Deer are the principal prey of wolves (Smith et al 1987, Kohira 1995, Person et al. 1996) and reductions in deer numbers will likely affect wolf populations. Of particular concern are the wolf and deer populations on Prince of Wales and Kosciusko Islands which may constitute 30-40% of the total wolf population in southeastern Alaska (Person et al. 1996). These islands comprise the most extensively logged areas and are targeted for future timber harvest because they have some of the most valuable forest stands in the



Figure 1. Map of southeastern Alaska.

region and much of the road and facility infrastructure needed for industrial-scale logging already exists. Clarence Strait, which separates Prince of Wales Island from the mainland, poses a significant barrier to immigration or emigration; therefore, the populations of deer and wolves on Prince of Wales and Kosciusko Islands likely are isolated from other populations in southeastern Alaska.

We describe the derivation and use of a simple predator-prey model to study the dynamics of the wolf-deer system on Prince of Wales and Kosciusko islands and to predict the demographic viability of the predator-prey system over the next century. Our objectives are to:

- 1) Model the predator-prey system incorporating those factors likely to have the most effect on the viability of the system.
- 2) Conduct a thorough sensitivity analysis of the model system and apply it to empirical data from other areas to validate outcomes from the model.
- 3) Apply the model to Prince of Wales and Kosciusko islands to predict the effects of timber harvest and human development on the persistence of the wolf-deer system.

We do not consider genetic influences or catastrophic events such as epidemics of disease. Therefore, outcomes from our model are the result of demographic processes and should be interpreted as such.

BACKGROUND

Distribution

Wolves are distributed throughout southeastern Alaska, from Dixon Entrance in the south to Yakutat Bay in the north (Figure 2). The islands in the southern portion of the archipelago support most of the wolf population. Indeed, 30 to 40% of the total wolf population may occur on Prince of Wales Island alone, the largest island in the archipelago (Person et al. 1996). Wolves are not found on Admiralty, Baranof, and Chichagof (ABC) islands in the northern part of the archipelago. Based on analysis of the capability of habitat to support prey, population densities on the mainland are thought to be lower than those on the islands (Person et al. 1996). Wolf harvest statistics tend to support this conclusion (Figure 3).

In the southern half of the archipelago, only the largest islands -- Prince of Wales, Kuiu, Kupreanof, Mitkof, Etolin, Revillagigedo, Kosciusko, and Dall -- and the mainland probably support permanent populations of wolves (i.e., over the last 40 years).

Persistence also varies within island groups. For example, in GMU 2 (Game Management Unit, an Alaska Department of Fish and Game [ADFG] designation) only the three largest islands -- Prince of Wales, Kosciusko, and Dall -- are known to have been continuously occupied by wolves for more than 20 years. Groups of smaller islands (e.g., Baker, Lulu, and Noyes) are used by wolf packs but are probably too small to support packs permanently (Person and Ingle 1995).

Southeastern Alaska wolf populations are separated from interior Alaska and Canada by the heavily glaciated Coast Mountains, which are breached by only six rivers or passes. Wolves occur in these valleys but the degree of interchange between interior and coastal populations is unknown, though it is probably small. Wolves are known to be able to swim distances of up to 4 km (Person and Ingle 1995). Nonetheless, distance, strong

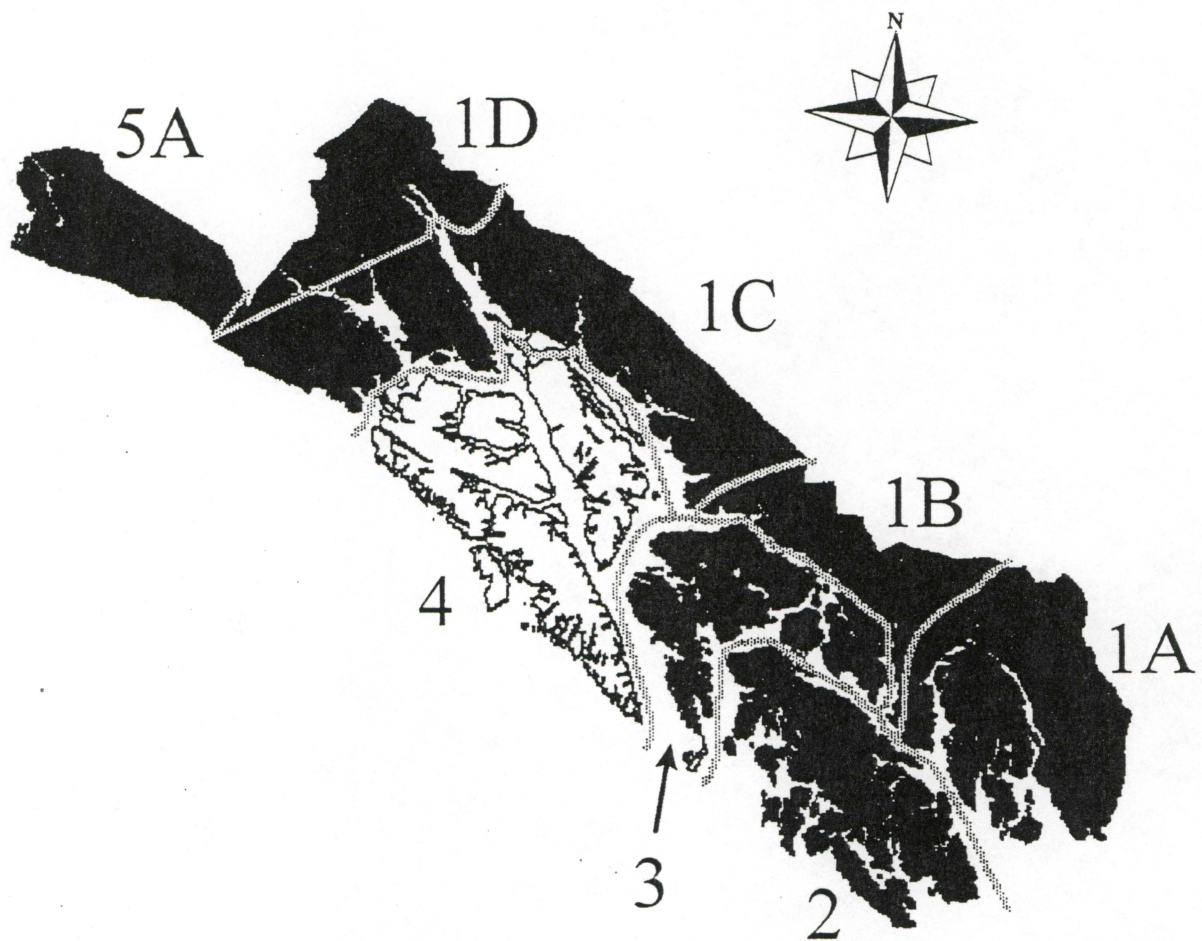


Figure 2. Map showing range of the Alexander Archipelago wolf (black areas) and Game Management Units (GMUs) in southeastern Alaska.

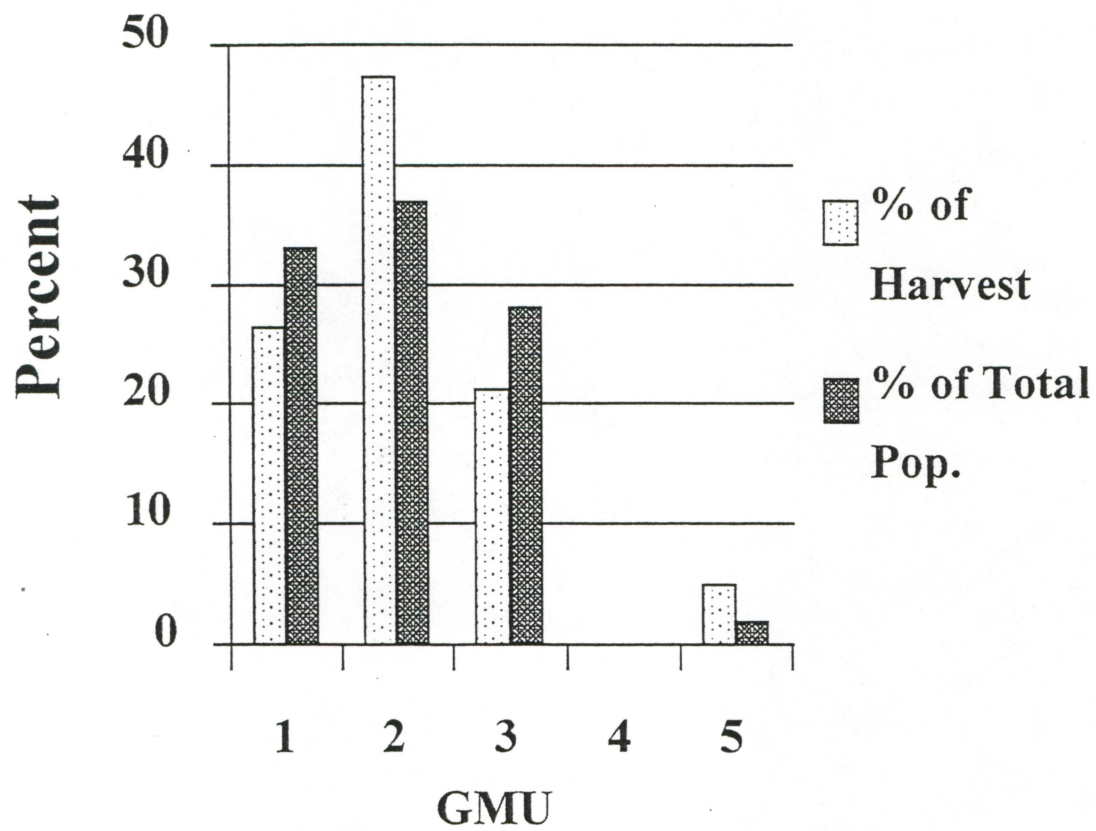


Figure 3. Histogram showing the distribution of the wolf population and reported harvest by Game Management Unit (GMU).

currents, and frequent bad weather would likely limit the frequency of migrations between island groups and the mainland. Frederick Sound, Stephen's Passage, and Icy Strait prevent immigration to the ABC islands, for example. In the south, Clarence Strait most likely restricts movement from the mainland to Prince of Wales Island. A series of stepping-stone islands could serve as a conduit, but at least eight directed swims would be required for this crossing, making it unlikely to occur very frequently. In some areas such as the Stikine River delta, short open-water distances at low tide may enable movements between some islands and the mainland (Person et al. 1996).

Taxonomy

The Alexander Archipelago wolf is generally smaller, darker in normal coloration, and shorter-haired than other wolves in Alaska. It was first described as a subspecies (*C. l. ligoni*) by taxonomist E. A. Goldman on the basis of morphological characteristics of skulls and other physical characteristics (Goldman 1944). More extensive morphometric analyses suggested that the Alexander Archipelago wolf is indeed distinct from wolves in the interior regions of Alaska and Canada (Pederson 1982), but may be related to wolves from coastal British Columbia and Vancouver Island (Nowak 1983, and Friis 1985).

A recent taxonomic revision proposed by Nowak (1995) groups the Alexander Archipelago wolf with *C. l. nubilus*, a subspecies that currently occurs in central Canada and Minnesota but formerly extended across much of the northwestern U.S. The Alexander Archipelago wolf is thought to have followed Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) north from the Pacific Northwest following retreat of the Wisconsin glaciation from southeastern Alaska (Klein 1965a). This hypothesis is supported by Nowak's (1995) inclusion of these wolves with historic populations in coastal British Columbia and the Pacific Northwest.

Genetics

A preliminary genetic analysis of mitochondrial DNA (mtDNA) from southeastern Alaska wolves identified a fixed allele within a 310 base-pair portion of the control region that may be used to distinguish these wolves from others in interior Alaska and the Yukon (Shields 1995). In addition, Alexander Archipelago wolves failed to exhibit variation at eight other nucleotide sites that were polymorphic in wolves from interior Alaska and the Yukon. These data are consistent with the morphometric data provided by Pedersen (1982), Friis (1985), and Nowak (1995) and may support the hypothesis of a southern origin for the Alexander Archipelago wolf.

Although, recent studies (Kennedy et al. 1991, Wayne et al. 1992) suggest that North American wolves may be a single large population, none of these studies included the Alexander Archipelago wolf. Published information concerning wolf genetics has focused primarily on results from allozyme electrophoresis of nuclear DNA (Kennedy et al 1991) and restriction fragment analysis of mtDNA (Wayne et al. 1992). Studies that directly sequence hypervariable regions of mtDNA or that employ nuclear markers may be needed to adequately address the issue of phylogenetic relationships amongst wolves.

The genetic data that are currently available do not demonstrate evidence of distinct subpopulations within the archipelago (Shields 1995). These results suggest that some degree of gene flow has occurred within the region in the past, but they are inadequate to determine whether and to what extent gene flow continues to occur among island groups and the mainland (Person et al. 1996).

Population Status and Trends

The wolf population of southeastern Alaska is currently estimated by Alaska Department of Fish and Game (ADF&G) to be about 1,200 wolves. This estimate is based on harvest

data and speculation by trappers, hunters, and biologists. The estimate is subjective and allows no assessment of accuracy or precision. Alternatively, Person et al. (1996) incorporated data on pack size, number of packs, home-range sizes, and reproductive rates into a simulation model to estimate seasonal populations for Prince of Wales and Kosciusko Islands (which probably function as one island because barriers between them are minimal). The estimates were refined by comparing them with observed wolf densities on the islands. This process resulted in a population estimate for autumn 1994 of 269 wolves (SE = 80) on Prince of Wales and Kosciusko Islands. For spring 1995 the estimate was 174 wolves (SE = 68), with the difference attributable to overwinter mortality, primarily from hunting and trapping.

Extrapolating the population estimate for Prince of Wales and Kosciusko islands to the rest of GMU 2 yielded an estimate of 336 wolves during fall 1994. Data on pack and home-range sizes are not available for the rest of southeastern Alaska, consequently, a model linking wolf numbers to habitat capability for deer and other prey (Suring and DeGayner 1988) was used to estimate the proportion of the total wolf population that GMU 2 probably represents. Game management unit 2 may support about 37% of the total wolf population in southeastern Alaska; therefore, the autumn 1994 total population estimate was 908 wolves ($336/0.37$, SE = 216, Person et al. 1996).

In a sample of radio-collared wolves on Prince of Wales and Kosciusko islands, mortality was estimated to be 61% (SE = 11%) during 1993-1994 and 38% (SE = 13%) during 1994-1995 (Person et al. 1996). Of the 24 radio-collared wolves, nine (38%) were legally killed during the trapping seasons, five (21%) were illegally killed by humans, and three (12%) died of natural causes. Analysis of birth and mortality rates for wolves on Prince of Wales and Kosciusko islands suggests that the finite rate of increase (λ) for wolves was less than one for the period between June 1993 and June 1995, indicating a decline in

population (Person et al. 1996). This result is consistent with observations by biologists and trappers that indicate the population peaked in 1992-93 and has declined since, primarily because of hunting and trapping. The wolf population in GMU 2 may be resilient because of adequate numbers of prey, and may quickly rebound if hunting and trapping pressure decreases. Data currently available are inadequate to assess population trends outside GMU 2.

Conservation Concerns

The Alexander Archipelago wolf population is small and exists in a naturally fragmented, insular environment that is changing radically and rapidly. An increasing human population plus the cumulative effects of road-building and habitat degradation may compromise the long-term viability of some segments of the wolf population and put the wolf on a collision course with human interests with respect to timber harvest and subsistence deer hunting. The major areas of concern are: habitat loss and fragmentation, mortality from exploitation by humans and the construction of roads that allow human access to previously roadless areas.

Habitat--Concerns for maintaining wolf habitat in the Tongass revolve around maintaining adequate habitat for deer, their primary prey. Deer constitute 70-80% of the diet of wolves on the islands and on some portions of the mainland (Smith et al 1987, Kohira 1995, Person et al. 1996). Deer are also important to human subsistence hunters. Consequently, sufficient deer habitat must be preserved to provide for both wolves and humans.

Old-growth forest stands are generally uneven-aged and structurally diverse with numerous vegetative layers (Alaback 1982, Alaback and Juday 1989). Intermittent openings in the forest canopy allow shrubs and forbs to develop near the forest floor,

where they are available to deer. Because the forest canopy intercepts snow, old-growth forest is particularly important for deer during winter when snow prevents foraging in open areas (Wallmo and Schoen 1980, Schoen and Kirchhoff 1985, Kirchhoff and Schoen 1987). Clearcut logging removes old growth and replaces it with even-aged second-growth forest (Alaback 1982). Clearcuts <20 years old can provide forage for deer during snow-free periods, however, the forage is typically of poorer nutritional value than that found under old-growth stands (Hanley and McKendrick 1985, Hanley et al. 1989). Twenty to thirty years after logging the second-growth forest canopy closes over and shades out vegetation growing on the forest floor, creating a virtual desert with respect to forage for deer (Wallmo and Schoen 1980). This condition lasts for at least 150-200 years before old-growth forest characteristics return (Wallmo and Schoen 1980, Alaback 1982). The current forest plan calls for 100-year harvest rotations (USFS 1997); therefore, once old-growth stands are cut they will probably never regain their original structure.

By 2090, logging will have removed approximately 40-50% and 30-40% of the commercially valuable old-growth forest growing on federal and private lands in GMUs 2 and 3, respectively. The overall capability of the habitat to support deer is expected to decline at least 20% from current levels in these GMUs (USFS 1997), which support 60-70% of the total wolf population in southeastern Alaska (Person et al. 1996). In the most intensively logged areas within GMUs 2 and 3, declines in deer habitat capability may be 50-70% (USFS 1997). The long-term consequences of such reductions in deer habitat may be to place the viability of some segments of the wolf population at risk and put wolves in direct conflict with human subsistence hunters.

Exploitation—Liberal hunting and trapping seasons contribute to the exploitation of wolves in southeastern Alaska. The trapping season extends from November to May with no bag limit, and up to five wolves per person may be shot during the hunting season

which begins in August and ends in May. Hunting and trapping seasons are regulated by the Alaska Department of Fish and Game and the Federal Subsistence Board.

Easy access and intense trapping effort have led to potentially unsustainable levels of mortality in some areas. Of most concern is GMU 2 where harvest rates may exceed 45% in some years when both legal and illegal killing is accounted for (Person and Ingle 1995). Mortality rates due to hunting and trapping will likely rise in GMU 2 because the human population is increasing rapidly along with greater access to wolves facilitated by the construction of roads associated with logging. The human population on Prince of Wales Island and the immediate area has increased from about 1,000 in 1960 to over 7,000 in 1995 (U.S. Census Bureau 1996). Since 1990 the population has grown 13% (U.S. Census Bureau 1996). This expanding population also carries with it an increasing demand for deer for sport and subsistence hunting.

Road Access—Logging roads present two problems for wolves in the Tongass. First, the existence of roads represents habitat loss from logging, although roads are used by wolves as travel corridors. Second, roads enable human access into the interior of islands that previously were only accessible by boat, resulting in increased wolf mortality. Although 55% of wolves in southeastern Alaska are trapped from the shoreline, in recent years a growing proportion (44%) has been trapped along the road system.¹

Since 1954, over 4,800 km (3,000 miles) of road have been built in GMU 2 (Prince of Wales and the immediately adjacent islands), primarily for logging. Under current Forest Service management plans, road building is expected to continue at a very high rate. For

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

example, if approximately 1 kilometer of road is constructed per 1.24 million board feet of timber removed (USFS 1997), about 1,800 kilometers of road in GMU 2 and 2,200 kilometers in GMU 3 will be built on Federal lands over the next century (USFS 1997, Figure 4). Road construction will also continue on private lands, however, estimates of the cumulative length are not available.

Game Management Unit 2, which includes Prince of Wales Island, is the area of most concern with respect to roads. GMU 2 is subdivided by ADFG into smaller Wildlife Analysis Areas (WAA) that are usually associated with individual watersheds. Over 70% of the WAAs in GMU 2 are accessible by road. Road densities in 50% of WAAs in GMU 2 exceed 0.6 km/km^2 , the density of road suggested by researchers in other areas of North America to be inimical to wolves (Jensen et al. 1986, Mech et al. 1988, Mech 1989). Wolves in GMU 2 use heavily roaded landscapes, but pack core areas are located in the least densely roaded portions of home ranges. Wolf harvest rates were significantly higher in more densely roaded WAAs in GMU 2 and harvest rate was related to length of road within a WAA, regardless of the size of WAAs (Person et al. 1996). Reported wolf harvest doubled when the length of road exceeded 95 km, corresponding to a road density of 0.4 km/km^2 of road below 370 m elevation (Person et al. 1996). Wolves spend most of their time at low elevation and road density calculations should reflect this relation (Person et al. 1996).

Many logging roads are scheduled to be closed following timber harvest but are left open to allow additional harvest or thinning. Attempts by the Forest Service to close roads have been ineffectual in many instances and road closure policy has not been systematically applied. Moreover, physical barriers (e.g., pulled culverts) can be avoided by people on ATVs or snowmachines. In 1990 the Alexander Archipelago wolf was identified by an interagency committee as one of eight species potentially at risk on the

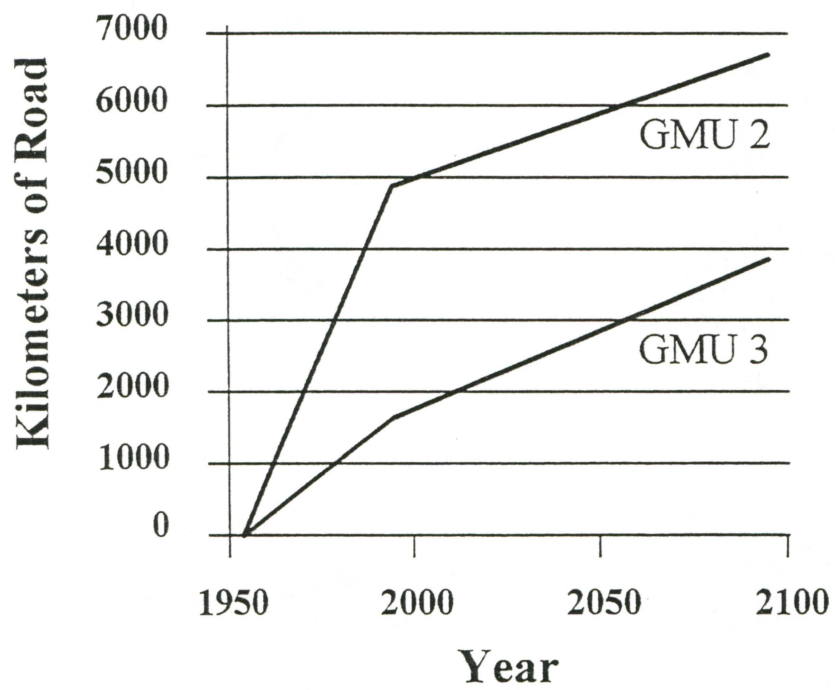


Figure 4. Estimated linear kilometers of road in GMUs 2 and 3 (USFS 1997).

Tongass National Forest (Suring 1993). In 1993 the Biodiversity Legal Foundation petitioned the U. S. Fish and Wildlife Service to list the Alexander Archipelago wolf as threatened under the Endangered Species Act, citing habitat loss from clearcutting, road construction in wolf habitat, hunting and trapping, and inadequate state and federal regulatory mechanisms as threats to the wolf population. The petition was denied in 1994, in part because the Fish and Wildlife Service anticipated opportunities to work with the Forest Service to maintain viable wolf populations and habitat through modifications of the Tongass Land Management Plan (TLMP) (USFWS 1994). The petitioners successfully sued the U. S. Fish and Wildlife Service over the negative finding in 1996 and the agency was ordered to do a new status review and reconsider their decision. In August 1997, the U. S. Fish and Wildlife Service determined that a listing was not warranted because of provisions for the conservation of wolves in the revised Tongass Land Management Plan.

METHODS

Model Building

Classical population viability analysis (PVA) generally employs the following approaches:

- 1) analysis of long-term time series data with emphasis on rates of increase.
- 2) analysis of age-specific rates of mortality and reproduction and the application of age-structured models such as the Lotka-Leslie model to identify the critical components influencing changes in population.
- 3) construction of population models (spatially explicit or otherwise) to simulate populations and predict changes due to variable inputs.

The first two strategies require long-term time series data that are not available for wolves in southeastern Alaska. Nonetheless, much is known about the population dynamics of wolves in relation to prey from studies in other areas and data are available to make reasonable estimates of some population parameters for wolves and deer in southeast Alaska; therefore we chose the third approach.

Viability analyses of wolf populations have typically concluded that adult and pup survivorship is the most important factor to be addressed with respect to the conservation of small wolf populations (Ciucci and Boitani 1991, Haight *pers comm.*). This is primarily because most PVAs treat the population dynamics of wolves as a birth-death process in which demographic rates are random variables. As an example, consider the general form of the Lotka-Leslie model, which is commonly employed in age-structured population models used in viability analyses:

$$l = \sum_{x=0}^{\infty} \frac{l_x b_x}{\lambda^x}$$

where

l_x = survivorship of wolves to age class x ,

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

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

Person et al. (1996) modified this model for use with wolves such that

$$0 = \lambda^3 - s\lambda^2 - s_0s_1b_2\lambda - s_0s_1s(b - b_2)$$

where

s_0 = rate of survival for juveniles,

s_1 = rate of survival for subadults,

s = rate of survival for adults,

b_2 = number of female offspring per female at age = 2 years, and

b = number of female offspring per female >2 years old.

If birth rates for all age classes are assumed to be equal the model simplifies to

$$0 = \lambda^3 - s\lambda^2 - s_0s_1b\lambda.$$

For a stationary population, $\lambda = 1$; therefore,

$$\frac{1-s}{s_0s_1} = b.$$

The quantity $1 - s$ is the same as the rate of mortality (m), hence

$$\frac{m}{s_0s_1} = b.$$

A small change in the survival rate of juveniles or subadults will require a large change in b if a stationary population is to be maintained. For example, if $s_0 = 0.5$, $s_1 = 0.7$, and $s = 0.8$, b must equal 0.57; whereas, if all survival rates decrease 10%, b must equal 0.99, a 74% increase, if a stationary population is to be maintained. Clearly, the model is most sensitive to the rates of survival. Nonetheless, rates of birth and survival are not random variables in an actual population of wolves. They are partly determined by the availability of prey and are likely to be correlated. For example, in an unexploited wolf population, if prey availability is low, survival rates may be low and fewer pups produced as well. Conversely, if prey are abundant, both survival and reproduction may increase resulting in a rapidly growing wolf population. Typical PVA models usually do not account for the behavioral adaptations of wolves to changes in the number of prey or wolves. For example, if the density of prey is high and wolves are heavily exploited, two or more females in a pack may produce pups, increasing the birth rate dramatically. Thus, a classical analysis of populations may predict a declining wolf population due to the low survival rates when in fact the population is actually remaining stable.

We constructed a relatively simple population model for wolves and deer on Prince of Wales and Kosciusko islands that allows us to simulate the effects of factors likely to influence wolf numbers, namely declining deer carrying capacity, road construction, and human exploitation. The model is a mathematical translation of the concepts relating to wolf population dynamics accepted by most biologists working with wolves. It was subjected to extensive sensitivity analyses to eliminate unnecessary or redundant parameters and calibrated for the conditions that currently exist on Prince of Wales and Kosciusko islands. The model was then simulated using Monte Carlo techniques while applying various scenarios in which deer carrying capacity, length of roads, and harvest rates were changed to be consistent with TLMP alternatives 1, 9, and 11. Further, a pre-1954 scenario was simulated to serve as a control.

Model Assumptions

Deer Model--

- 1) Deer populations exhibit density-dependent population growth that can be approximated by a theta-logistic function such that the product of parameter r_{max} and the density-dependent modifier represents recruitment and all compensatory mortality in the absence of predation and hunting (Person et al. *in review*).
- 2) Mortality from predation and hunting is primarily additive (Gasaway et al. 1992, Hayes 1995) and the 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), the effects of density-dependent predation rates are small unless the prey population is at very low density (Person et al. *in review*). 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.

3) The model does not consider the sex and age structure of the adult deer population. All sex and age-classes are equally vulnerable to predation and the sex ratio at birth is considered to be 1:1.

4) The model assumes that deer are removed first by wolf predation and hunting is allocated what is left. Wolves prey on deer year-round and kill both sexes. Hunting occurs for 5 months beginning in August and primarily removes adult males from the deer population. Further, the legal hunting bag limit is 4 deer per year. Predation by wolves will have a much greater impact on deer than 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. Our assumption tends to present an optimistic scenario for wolves when deer populations are low.

Wolf Model--

1) Wolf population dynamics on Prince of Wales Island are primarily a function of the availability of deer biomass (Keith 1983, Fuller 1989, Gasaway et al. 1992). The age structure of wolf packs is not considered in the model.

2) Litter size, dispersal and natural mortality are density-dependent with respect to the ratio of deer biomass available to wolves (Keith 1983, Boertje and Stephenson 1992). Natural mortality rates and dispersal rates are compensatory with mortality from trapping or hunting (Fuller 1989).

3) All dispersers have equal probability of successful immigration regardless of distances traveled within the island system. Packs containing >1 wolf will not assimilate dispersers

and pack territories that have insufficient prey to support >2 wolf do not produce litters or assimilate dispersers.

4) Wolf and deer populations on Prince of Wales and Kosciusko Islands are closed with an insignificant probability of dispersal to and from the area.

5) The model assumes that a 2-year time lag exists in the response of wolves to changes in deer populations. The time lag represents the buffering effect of alternative prey such as beaver (*Castor canadensis*), marine mammals, and fish on wolf populations. This is consistent with data from wolves on Isle Royale (Peterson and Page 1988).

Description of Deer Model

$U_{t(i)}$ = Spring deer population prior to parturition in vicinity of area(i)

$$R_{ut(i)} = \text{recruitment} = U_{t(i)} r_{\max} \left[1 - \left(\frac{U_{t(i)}}{K_{t(i)}} \right)^{\theta} \right] \quad (1)$$

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 in the vicinity of area(i).

$CP_{at(i)}$ = predation mortality

C = deer killed per wolf per year.

$P_{at(i)}$ = average wolf population in year t in area (i) = $(P_{t(i)} + (P_{t(i)} + R_{pt(i)}))/2$

$H_{t(i)}$ = deer harvest = $U_t h (1 + 0.038 * Km \text{ Roads})$

h = base harvest rate in the absence of roads.

$$U_{t+1(i)} = U_{t(i)} + R_{t(i)} - CP_{at(i)} - H_{t(i)} \quad (2)$$

$$\text{Total deer population} = U_t = \sum_{i=1}^j U_{t(i)} \quad (3)$$

j = number of areas.

Description of Wolf Model

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

$$R_{pt(i)} = \text{recruitment to pack}(i) = b \left[1 - \frac{CP_{t(i)}}{\alpha U_{t-2(i)}} \right] \quad (4)$$

b = average litter size when the ratio of prey: wolves is very high.

α = proportion of deer population actually available to pack in area(i).

$$T_{t(i)} = \text{wolves harvested from pack in area}(i) = t (P_{t(i)} + R_{pt(i)})(1 + 0.0046 * Km \text{ Roads})^2$$

t = base harvest rate in the absence of roads.

$$\dot{D}_{t(i)} = \text{dispersal from pack in area}(i) = (P_{t(i)} + R_{pt(i)} - T_{t(i)}) \left[d \left(\frac{CP_{t(i)}}{\alpha U_{t-2(i)}} \right) \right] \quad (5)$$

d = base dispersal rate at equilibrium.

$$M_{t(i)} = \text{natural mort. in pack in area}(i) = (P_{t(i)} + R_{t(i)} - T_{t(i)} - D_{t(i)}) \left[m \left(\frac{CP_{t(i)}}{\alpha U_{t-2(i)}} \right) \right] \quad (6)$$

m = base mortality rate at equilibrium.

$$I_{t(i)} = \text{immigration to area}(i) = \begin{cases} 1 \text{ or } 2, P_{t(i)} < 2 \text{ and } D_t > 0 \text{ and } \frac{CP_{t(i)}}{\alpha U_t} > 2 \\ 0, \text{ otherwise} \end{cases} \quad (7)$$

$$D_t = \text{total dispersers in population} = s_d \sum_{i=1}^j D_{t(i)} - \sum_{i=1}^j I_{t(i)} \quad (8)$$

s_d = annual survivorship for dispersers.

$$P_{t+1(i)} = P_{t(i)} + R_{pt(i)} - T_{t(i)} - D_{t(i)} - M_{t(i)} + I_{t(i)} \quad (9)$$

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

j = the number of areas.

Description of Models Used to Simulate the Effects of Roads

Wolf Harvest v Roads--Regression of the square root of the average wolf harvest (1990-1995) against the linear kilometers of road within a Wildlife Analysis Area (WAA) produced the following result (Person et al. 1996):

$$\sqrt{\text{Average Wolf Harvest (1990 - 1995)}} = 0.84 + 0.0039(\text{Km Roads}); r^2 = 0.39, P = 0.0015.$$

Conversion of regression model to model of relative risk from road construction:

<u>Wolf Harvest</u>	<u>Roads (Km)</u>
0.71 (1X)	0
1.42 (2X)	89
2.13 (3X)	159
2.84 (4X)	217
3.55 (5X)	268
4.26 (6X)	314
4.97 (7X)	356
5.68 (8X)	396

Regression (1X...8X) versus roads (Km):

Harvest risk due to roads = $(1 + 0.0046 * Km\ Roads)^2 \pm 95\%$ prediction interval.

Deer Harvest vs Roads--Regression of average deer harvest (1990-1995) against the linear kilometers of road in a WAA produced the following result:

*Average Deer Harvest (1990-1995) = 14.7 + 0.553 * Km Roads; $r^2 = 0.65$, $P < 0.001$.*

Conversion of regression model to risk model:

<u>Deer Harvest</u>	<u>Roads (Km)</u>
14.7 (1X)	0
29.4 (2X)	27
44.1 (3X)	53
58.8 (4X)	80
73.5 (5X)	106
88.2 (6X)	133
102.9 (7X)	160
117.6 (8X)	186

Regression (1X...8X) versus roads (Km):

Harvest risk due to roads = $1 + 0.038 * (Km\ Roads) \pm 95\%$ prediction interval.

Sensitivity Analyses

We conducted a multiple parameter sensitivity analysis to determine which parameters were most influential and which were redundant. We evaluated the deer and wolf models separately. Each of the input variables was given a uniform distribution bounded by biologically reasonable maximum and minimum values. We simulated the models 1,000 times using Monte Carlo techniques in a full factorial design and then regressed the input parameters against the deer and wolf numbers predicted in each replication. We compared the standardized coefficients to determine the relative influences of each parameter on the outcomes (Neter et al. 1985).

The model estimates reproduction by assigning an annual litter to a pack within a pack area. Litter size varies stochastically with the mean of the sampling distribution dependent on the ratio of deer to wolves. Hence, litter size is partly of function of the habitat conditions for deer (K). The upper limit of litter size is sufficiently high to simulate packs that split or bud when prey conditions are very favorable (large K) and produce two litters simultaneously. The number of litters is dependent on the number of pack areas allowed, therefore, reproduction is scale-dependent. We tested the effects of spatial scale and on the model by simulating wolf and deer populations for which carrying capacity and the number of pack areas were fixed at various levels. Simulations were conducted for K equal to 1,680, 3,360, 5,040, 6,720, 8,400, 10,080, 11,760, and 13,440 deer. The number of pack areas was set at 3, 6, and 9 packs areas; therefore the simulations tested the effects of habitat richness (K) and spatial scale (pack areas) on model outcomes. We conducted 1,000 Monte Carlo simulations at each factor level.

Application of Wolf-Deer Model to Isle Royale and Coronation Island

We used the wolf-deer 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 by the model were consistent with empirical data. We simulated the model 1,000 times using Monte Carlo techniques for each case.

To simulate conditions on Isle Royale, we allowed a maximum of 2 pack areas (potentially 4-5 packs) for the 544 km² area, estimated carrying capacity for moose to be 2000 (about 200 moose higher than the current population [DelGiudice et al. 1997]), set predation rate equal to 9 (Keith 1983; [95% C. I. = ± 2.8]), let maximum rate of increase for moose equal 0.45 (Ctenlund and Sand 1994), and let θ vary over a uniform range between 1 and 3. The vulnerability of moose to predation is age-specific (Peterson and Page 1988), therefore, we allowed the parameter representing the percent of the moose population available to wolves to vary uniformly between 25-75%; a lower range than that used in the simulations for deer. Further, we simulated winters with an average frequency of one severe winter per decade. During severe winters, the percent of the moose population available to wolves was increased 20% to simulate the effect of deep snow on the vulnerability of moose to predation. The parameters used for wolves were the same as those used in the simulations of the wolf-deer model for Prince of Wales and Kosciusko islands.

Coronation Island is 79 km² in area and is located in southeastern Alaska. Sitka deer occur on the island but wolves appear to have been historically absent (Klein 1995). In 1960, four wolves were introduced to the island and in four years they reached a population peak of 13 animals. Deer numbers, which were probably at carrying capacity when wolves were introduced, declined precipitously until numbers were so low that wolves resorted to alternative prey (Klein 1995). By 1970, the wolf population had disappeared and deer numbers increased rapidly. We simulated the wolf and deer population on Coronation Island by setting carrying capacity for deer at 600 animals (the

maximum population estimate given by Klein [1995]) and introducing a population of four wolves. All of the other parameters were given the same values that were used in the simulations of the wolf-deer model for Prince of Wales and Kosciusko Island except that dispersal from the island was not permitted.

Scenarios Used In Simulations

General Description--We used the numbers for deer predicted by the Forest Service habitat capability model for Alternatives 1, 9, and 11 of the Revised Tongass Land Management Plan as the estimates of carrying capacity for our scenarios (USFS 1997). In addition, we used the 1954 habitat capability estimates to predict the historical carrying capacity for deer prior to the beginning of industrial-scale timber harvest in the region. The habitat capability numbers were adjusted to be consistent with our comparison of habitat capability with ADF&G pellet-group data (Appendix 1). We estimated the mileage of road by assuming 1 mile of road to be built for every 2 million board feet of timber harvested (USFS 1997). The estimates of carrying capacity and road mileage are for Prince of Wales and Kosciusko Islands only (Table 1). These islands represent about 80% of the land area in Game Management Unit 2.

Alternative 1 represents a continuation of the current condition with no further logging or road building occurring after 1996. Carrying capacity declines from 1954 levels and will continue to decline for 25 years after 1996; thereafter, it remains constant throughout the planning period. Alternative 9 represents the previous Forest Plan in which timber harvesting will continue at current levels and most of the remaining high-volume old-growth forest will be removed by 2095. Alternative 11 represents the revised Forest Plan (USFS 1997). For alternative 11, we create 8 pack areas that are consistent with the old-growth forest reserves described in the revised TLMP. No new road construction after 1996 occurs in those portions of the pack areas that overlap the proposed reserves. In

addition, carrying capacity declines in the reserves only to the extent consistent with timber harvest prior to 1996.

Simulating Winters--Based on temperature and precipitation data from the National Weather Service on Annette Island and Sitka, and data from ADF&G, it appears that approximately 6 winters per century may result in general declines in deer numbers in the southern portion of the Alexander Archipelago. These events seem to follow a random walk model (autocorrelation function $P > 0.05$) 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 the 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 one severe winter (Kirchhoff *pers. comm.*). Nonetheless, Klein (1965b) reported that winter mortalities due to malnutrition were lower in areas where deer were exposed to predation by wolves. Where predation occurs, deer are probably well below carrying capacity and may be more likely to survive a severe winter. Therefore, we selected a relatively optimistic scenario. The winters of 1969-1970 were included in each simulation and severe winters occurred randomly after 1996.

Table 1. Description of scenarios used in the simulations. The estimates of carrying capacity for deer represent preparturient numbers of deer.

	Initial K	1995 K	2095 K	2135K
1954 Condition	61,835	61,835	61,835	61,835
	No road construction.			
Altern. 1	61,835	50,593	48,501	48,501
	Three thousand miles of roads built by 1996, K continues to decline for 25 years after timber harvesting ends in 1996.			
Altern. 9	61,835	50,593	36,503	32,827
	K continues to decline for 25 years after timber harvesting ends in 2095. Three thousand miles of road built before 1996, two thousand miles of new roads projected to be built between 1996 and 2095 (roughly half the roads projected for GMUs 1A and 2).			
Altern. 11	61,835	50,593	43,993	41,218
	K continues to decline for 25 years after timber harvesting ends in 2095. Three thousand miles of road built before 1996, about 1,100 miles of new roads projected to be built between 1996 and 2095.			

Parameter Estimates Used in the Simulations--

$j = 26$ areas, determined as follows:

Area of Prince of Wales and Kosciusko Islands = 6808 Km².

Average pack home range = 280 Km² (Person et al. 1996)

Average fraction of overlap between packs = 0.04 (Person et al. 1996).

Number of potential areas = $6808 / (280 * (1 - 0.04)) = 25$ packs.

$j = 26$ pack areas to provide for an optimistic estimate of the number of packs.

K = USFS deer habitat capability values scaled lower to account for our estimate (USFS 1997, Appendix 1.) of how much deer HSI overestimates K . The USFS numbers were corrected by multiplying them by 1.09.

$U_0 = 0.75(K)$; the model is insensitive to initial conditions so this value is arbitrary. K represents the 1954 conditions (USFS 1997)

$r_{max} = 0.6$, based on data for mule deer (*O. hemionus*) (McCullough 1987).

$\theta = N(2, 0.3)$, 95% between 1.4 and 2.6; based on fitting curves to data presented by McCullough (1979, 1987).

$C = N(26, 4)$ (Person et al. 1996), 95% between 18 and 34.

$h = 0.012$, determined by calibrating the model to 1995 conditions in which the average deer harvest is about 2700 deer (ADF&G *unpublished data*).

$P_0 = N(5.6, 3)$, (Person et al. 1996), 95% between 0 and 11.6.

$b = N(6, 1.8)$ (Person et al. 1996), 95% between 2.4 and 9.6. Very large litter sizes (>8) may represent a single successful breeding pair or be interpreted as “pack budding” in which a pack splits into two breeding groups within the original pack area.

$\alpha = U(0.5, 0.9)$, assumes that 50-90% of the deer population is instantaneously available to wolves. Value is randomized between 0.5 and 0.9.

$t = 0.10$, determined by calibrating the model to 1995 conditions in which the average wolf harvest is about 75 wolves (ADF&G *unpublished data*).

$d = N(0.3, 0.09)$ (Person et al. 1996), 95% between 0.11 and 0.48 (high rates that create optimistic probabilities for recolonization of vacant territories).

$m = N(0.5, 0.15)$ based on review of the literature (Peterson et al. 1984, Peterson and Page 1988, Fuller 1989), 95% between 0.2 and 0.8.

$s_d = N(0.5, 0.15)$ based on review of the literature (Peterson et al 1984, Fuller 1989), 95% between 0.2 and 0.8 (values are generally lower than observed on Prince of Wales Island [Person et al. 1996] and are optimistic estimates).

We conducted two sets of 100 Monte Carlo simulations of the wolf-deer model for each Forest Plan alternative and for the 1954 conditions. The first set allowed a harvest of wolves to continue throughout the period covered by the simulations. The second set curtailed the harvest of wolves after 1996 which would be consistent with the protections afforded them if they were listed under the Endangered Species Act of 1973 as amended.

RESULTS

Sensitivity Analysis

Results from 1,000 Monte Carlo simulation indicate that the deer model is most sensitive to the ratio of deer numbers (U) to K , the shape of the density-dependent function (θ) and the number of wolves (P) (Table 2). Although predation rate (C) and r_{\max} were significant parameters, their influence was overwhelmed by the proximity of the deer population to K , θ , and P . The human harvest rate (h) has a insignificant effect on the model. Clearly, changes in K will have a strong effect on the number of deer even when wolf predation exerts a significant influence.

The wolf model is most sensitive to deer numbers (U) and mortality due to trapping (Table 3). Other influential parameters are the percent availability of deer (α), the number of wolves (P), and predation rate (C). Although significant, the effects of litter size (b), and natural mortality (m) are minimal. Dispersal rate (d) is not significant mainly because dispersers suffer from high mortality and because those that survive generally settle and are accounted for by P . The low ranking of natural mortality is likely because it is compensatory with trapping mortality and has little influence on wolf numbers unless trapping is eliminated. The behavior of the model is consistent with the accepted notion that wolf numbers are more or less directly related to prey density.

The analysis of the effects of the interaction of spatial scale and K on the wolf-deer model indicated that the number of pack areas allowed (analogous to patch or island size) for a particular carrying capacity for deer has a significant effect on the equilibrated population of wolves predicted by the model (Figure 5). When the number of packs areas was restricted (thus, reproduction is constrained by a fewer number of packs) the wolf population at equilibrium was higher at low to moderately high carrying capacities for deer. This is because the number breeding wolves increases with the number of pack areas and

Table 2. Results of multiple regression of input parameters against deer numbers predicted by Monte Carlo simulations of equation (2).

Model Parameter	Stand. β	t	P
U/K	0.921	120.9	0.000
P	-0.268	-35.1	0.000
θ	0.125	16.4	0.000
r_{max}	0.088	11.6	0.000
C	-0.076	-9.9	0.000
h	-0.009	-1.1	0.266

Table 3. Results of multiple regression of input parameters against wolf numbers predicted by Monte Carlo simulations of equation (9).

Model Parameter	Stand. β	t	P
U	0.596	34.4	0.000
t	-0.396	-22.9	0.000
α	0.247	14.3	0.000
P	0.243	14.1	0.000
C	-0.209	-12.0	0.000
b	0.194	11.2	0.000
m	-0.054	-3.1	0.002
d	0.008	0.5	0.649

competition for prey increases rapidly. Hence, the limited number of prey are depleted more quickly as the number of wolves increases and populations of wolves and deer are more likely to fluctuate widely with an increased risk of going extinct. As K increased from moderate to high carrying capacities, the number of wolves at equilibrium increased rapidly along with the number of pack areas because sufficient numbers of deer existed to support a greater number of breeding individuals (Figure 5). The effect of a larger number of pack areas is to suppress the number of wolves at low carrying capacities but to significantly increase the number of wolves at equilibrium when carrying capacity is high. The standard error about the mean population of wolves at equilibrium increased with the number of pack areas suggesting that the predator-prey system may become more volatile (Figure 5). Indeed, the mode for the number of years required for the initial population of 2 wolves to reach its maximum level was 10 when the number of pack areas was restricted to 3 but only 5 when the number of pack areas was 6 or more. Hence, the rate at which wolves will respond to perturbations of the density of deer will be more rapid if more packs are involved. Clearly, it is important that the number of pack areas be estimated realistically when the model is applied to a specific set of conditions.

Application of the Model to Isle Royale and Coronation Island

Beginning with a single pair of wolves, the moose and wolf populations on Isle Royale were simulated for a 50-year period (Figure 6). The median wolf population in spring (before pups were born) after 3 years was 13 animals (populations in fall were about 20-30% larger). After the first 20 years the median spring population was 24 wolves. The maximum number of wolves predicted for any particular year was 53 and the minimum was 0. Only 1% of the simulated populations went extinct during the 50-year period. The median preparturient population of moose after 20 years was 1432 animals and the range was 45 to 2000 moose.

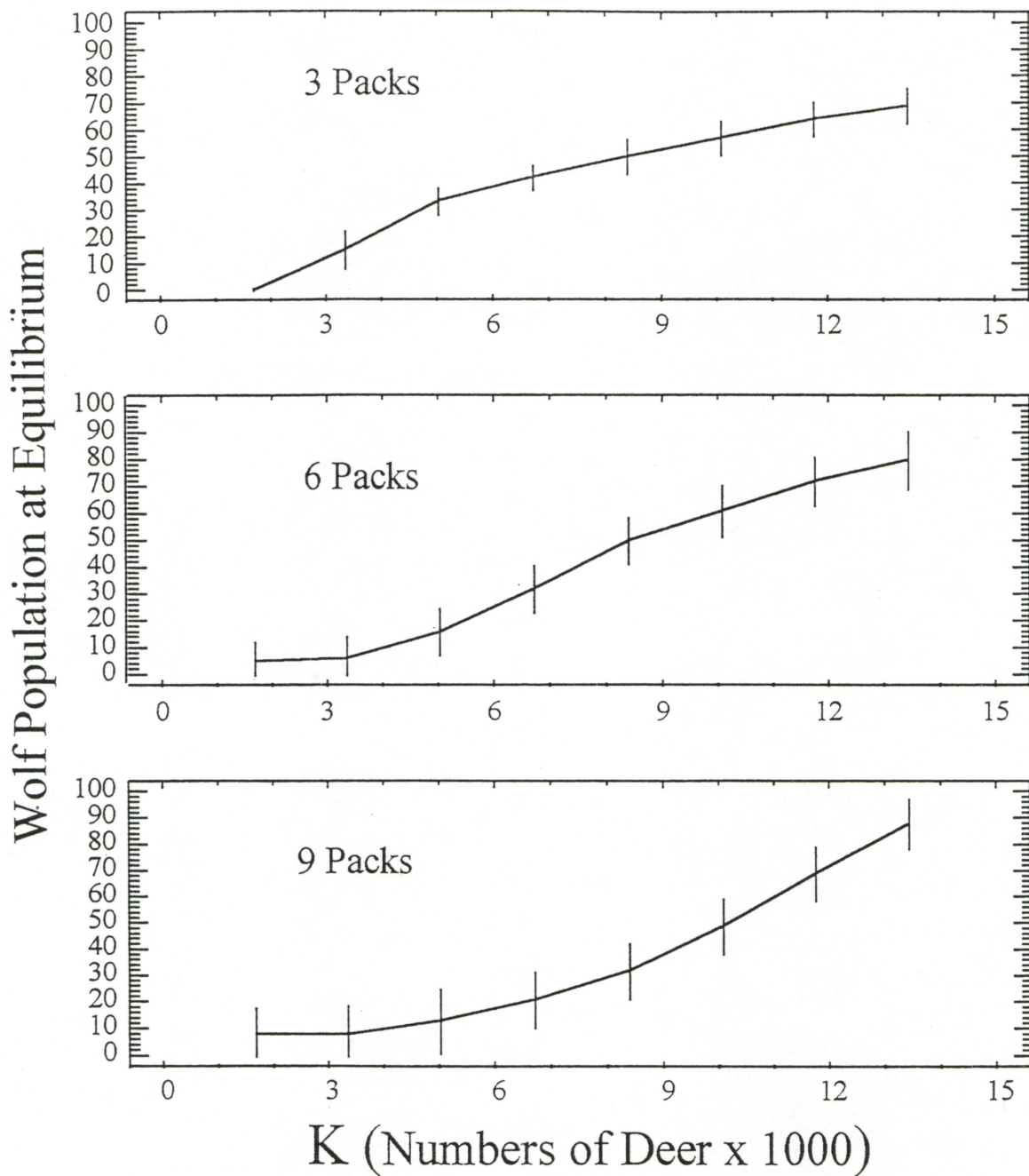


Figure 5. Plots showing the effects of K and the number of pack areas on the number of wolves at equilibrium. Increasing the number of pack areas is analagous to increasing the area of a patch and changes in K represent changes in the quality of a patch.

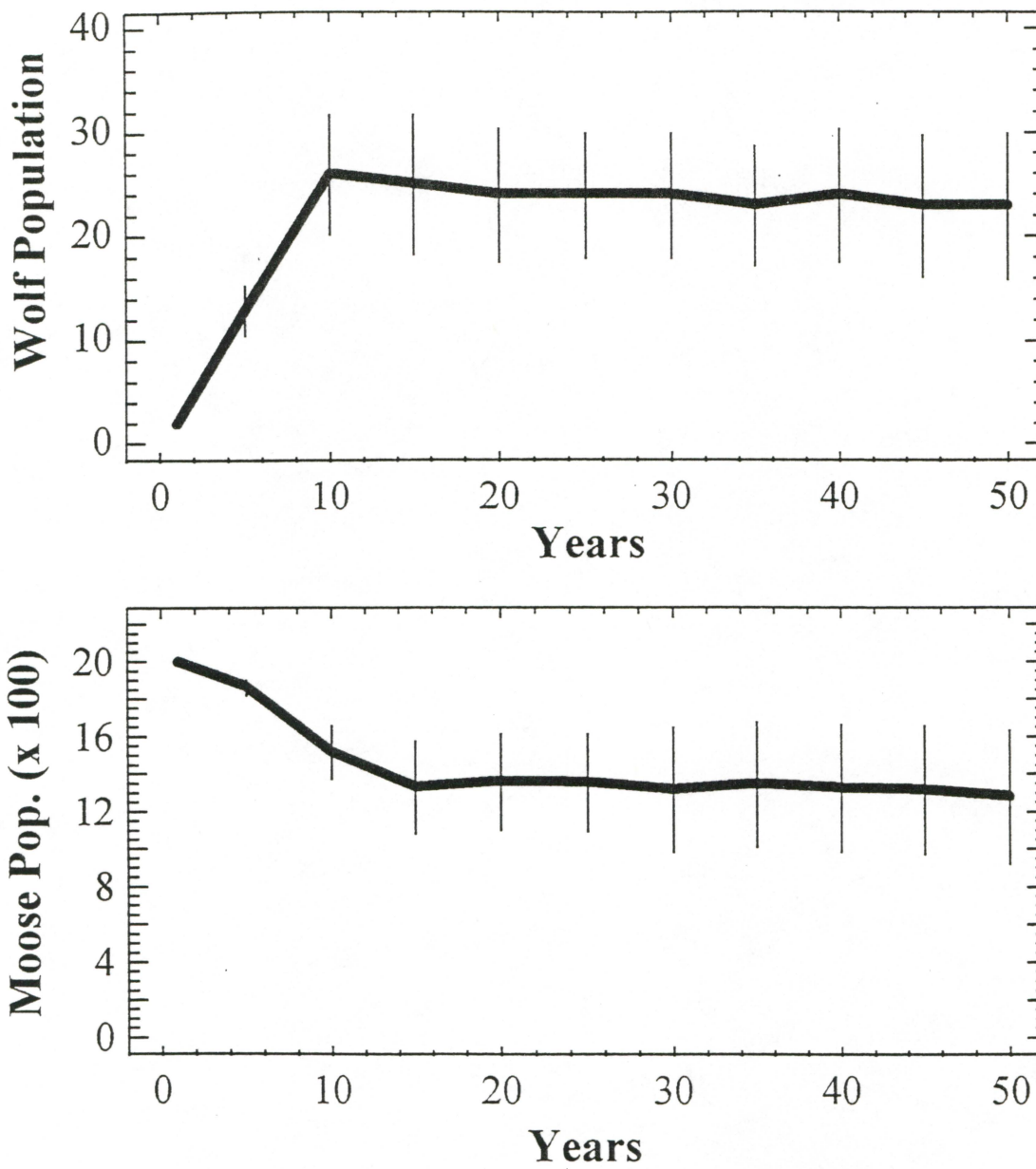


Figure 6. Simulations of the wolf and moose populations on Isle Royale, Michigan. Shown are the mean populations for all iterations of equations 3 and 10 with the vertical bars representing the standard errors.

The actual wolf population on Isle Royale has generally ranged between 14 and 25 wolves with a short-lived population surge occurring in the late 1970's (Peterson and Page 1988). The population reached a maximum of 50 wolves in 1980 and then crashed to 14 wolves by 1983. Median populations predicted by the wolf-deer model are close to the actual population levels. The moose population on Isle Royale fluctuated dramatically between 1960 and 1995, with lows of about 500 animals and highs close to 2000 moose (DelGiudice et al. 1997). The median population for the last 20 years has been well above 1000 moose in winter and is consistent with predictions from the model.

Model simulations for Coronation Island showed the number of wolves increasing from a propagule of 4 animals to a median population of 13 wolves in 3 years, followed by a precipitous decline to extinction (Figure 7). The actual population of wolves took 4 years to reach a peak of 13 animals and then declined to one wolf 3 years later (Klein 1995). The wolf-deer model generally predicted a more rapid increase in wolves than was actually observed; nevertheless, 2 of the 4 wolves introduced to Coronation Island were shot after the first year and this may have delayed the growth of the population.

The model predictions are reasonably consistent with empirical data from Isle Royale and Coronation Island. Populations predicted by the model tend to fluctuate more widely than the actual populations because the probability distributions of the input parameters incorporate greater variability than would be observed in most real populations. The standard errors of the input parameters reflect intrinsic variability as well as the uncertainty associated with the means of the distributions owing to limited data.

Simulation of Populations on Prince of Wales and Kosciusko Islands

The wolf-deer model was simulated 100 times using Monte Carlo techniques to predict wolf and deer populations on Prince of Wales and Kosciusko islands (Table 4) for a period

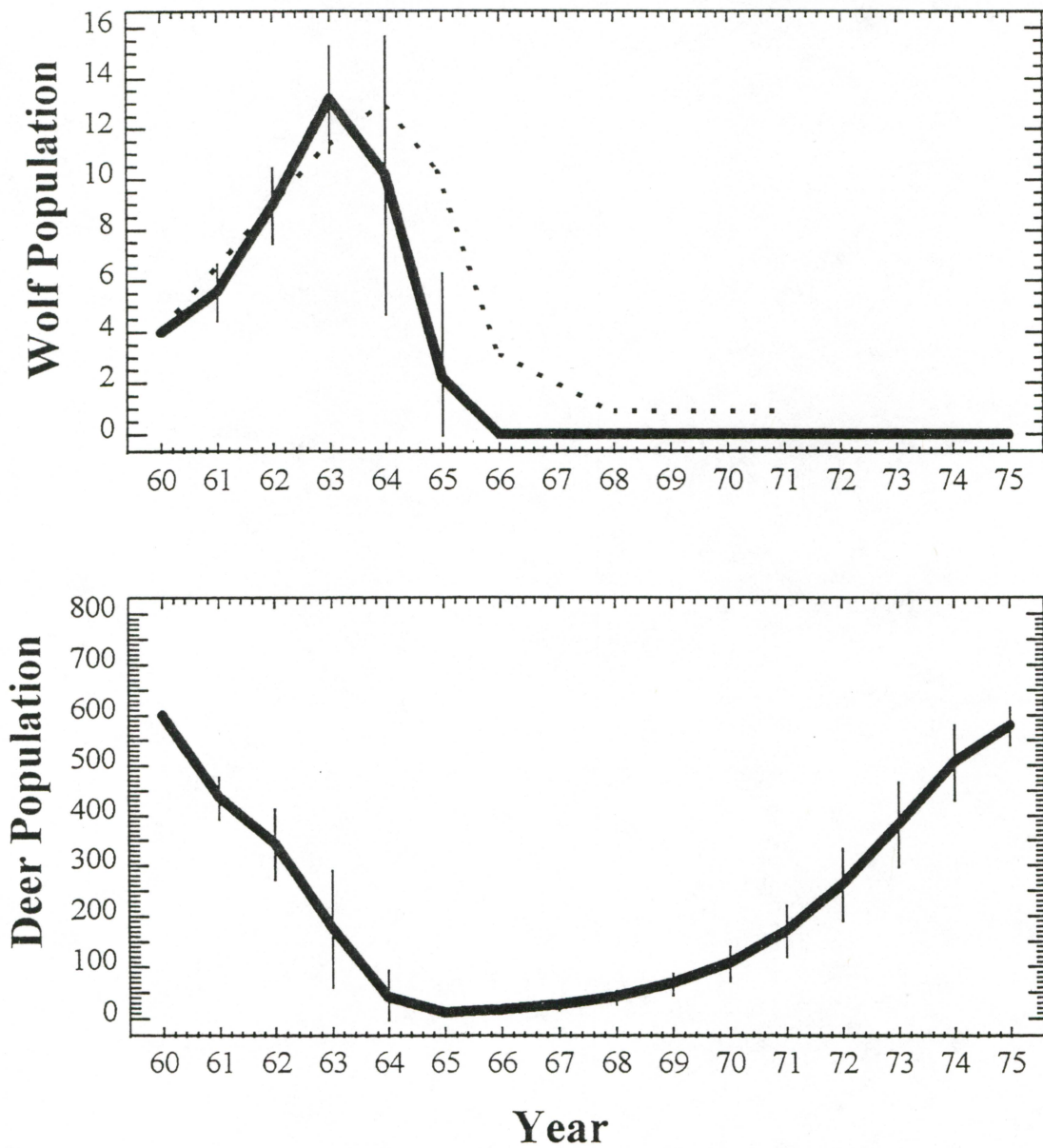


Figure 7. Simulations of the wolf and deer populations on Coronation Island. Solid lines show the mean population predicted by equations 3 and 10, the dotted line represents the actual wolf population observed after the experimental introduction of wolves in 1960. The vertical bars show the standard errors of the populations predicted by the model.

Table 4. Results of Monte Carlo simulations ($n = 100$) of the wolf-deer model showing the mean spring preparturient deer and wolf populations at 20-year intervals from 1955-2135. Each scenario was simulated with a wolf harvest allowed and with harvest terminated after 1997; winters were simulated for all scenarios. The number of packs remaining in 2135 is shown.

Deer Populations										
	1955	1975	1995	2015	2035	2055	2075	2095	2115	2135
1954 Conditions/ wolf harvest	48611	40578	49225	47571	47354	47450	47644	46798	46994	46931
SD	1498	2238	1698	4200	4667	4128	3988	4311	4917	5120
Minimum Pop.	44638	34615	45757	28246	27604	28955	30521	30992	18148	22453
1954 Conditions/ no harvest	48370	40044	49337	42285	41690	40910	40833	39182	39516	38316
SD	1643	2291	1468	7268	6414	6706	7043	7239	6747	6844
Minimum Pop.	43010	33157	46284	14325	21757	18147	12027	19339	20328	19838
Alternative 1/ wolf harvest	48037	35334	39958	33715	31556	30229	29447	28857	28948	26562
SD	1604	2522	1578	4117	3944	5063	4642	5453	4498	5242
Minimum Pop.	44136	29138	36690	14452	21077	11001	13422	11460	12824	10400
Alternative 1/ no harvest	48104	35672	39960	24092	20938	18278	17070	16956	16065	14941
SD	1751	2085	1352	4148	5282	3702	3693	3726	3155	3416
Minimum Pop.	44609	30766	36030	15280	8654	9583	8844	8900	10002	3191
Alternative 9/ wolf harvest	48519	35068	38120	33162	29730	25571	21879	18277	15246	13287
SD	1515	2446	1162	3506	3170	3780	4035	3534	2952	2991
Minimum Pop.	43507	29868	34622	21229	18996	16260	7764	8145	5299	5315
Alternative 9/ no harvest	48663	34764	38146	21052	16953	13338	10294	7915	6734	5964
SD	1616	2057	1550	4967	3599	3583	2865	2324	1901	1732
Minimum Pop.	43592	27582	34206	9245	10242	3797	2378	2132	2531	1337
Alternative 11/ wolf harvest	47442	34785	37455	33409	30751	30040	27062	25366	23448	22731
SD	2213	1776	1778	4029	4723	3844	4300	4391	4034	4077
Minimum Pop.	35964	30779	29271	21866	17502	19961	16246	13221	9490	10472
Alternative 11/ no harvest	48193	34802	38036	20734	18642	16551	14237	12398	11435	10511
SD	1527	2035	1197	5717	4918	3504	3757	2891	3009	2326
Minimum Pop.	45012	30827	34936	7905	4352	10610	4838	6008	6287	6519
Wolf Populations										
	1955	1975	1995	2015	2035	2055	2075	2095	2115	2135
1954 Conditions/ wolf harvest	320	253	312	301	306	306	301	303	300	300
SD	17	19	20	25	23	21	25	26	28	27
Minimum Pop.	284	200	263	216	243	246	196	207	112	166
1954 Conditions/ no harvest	321	253	311	351	359	341	344	328	327	319
SD	19	20	18	50	47	61	54	60	58	56
Minimum Pop.	322	255	309	366	371	363	360	339	337	325

Table 4 Continued.. Wolf Populations

Wolf Populations										
	1955	1975	1995	2015	2035	2055	2075	2095	2115	2135
Alternative 1/ wolf harvest	319	211	213	197	192	181	175	171	170	163
SD	17	18	15	20	21	23	22	26	22	25
Minimum Pop.	270	171	181	132	137	98	106	88	99	77
Alternative 1/ no harvest	318	218	214	229	204	184	173	168	166	150
SD	17	19	15	39	50	43	44	47	40	41
Minimum Pop.	279	177	184	135	79	87	66	48	86	46
Alternative 9/ wolf harvest	319	212	212	190	171	150	128	110	99	89
SD	18	18	17	20	19	22	21	22	19	20
Minimum Pop.	263	176	157	113	110	91	80	57	51	42
Alternative 9/ no harvest	317	213	210	205	182	146	123	107	98	93
SD	17	19	16	47	38	40	36	32	34	34
Minimum Pop..	274	167	166	69	107	34	38	41	26	12
Alternative 11/ wolf harvest	322	212	212	194	183	171	158	146	140	137
SD	20	20	15	19	22	26	23	21	23	21
Minimum Pop.	264	157	171	153	120	66	76	88	68	75
Alternative 11/ no harvest	317	213	213	209	188	171	154	143	132	128
SD	18	18	17	49	47	41	40	37	34	34
Minimum Pop.	274	176	168	37	66	48	31	54	63	58

Number of Packs in 2135					
1954 Conditions/ wolf harvest	25	1954 Conditions/ no harvest	22	Alternative 1/ wolf harvest	20
SD	1	SD	3	SD	3
Minimum	15	Minimum	12	Minimum	10
Alternative 1/ no harvest	13	Alternative 9/ wolf harvest	14	Alternative 9/ no harvest	8
SD	3	SD	3	SD	3
Minimum	13	Minimum	7	Minimum	2
Alternative 11/ wolf harvest	19	Alternative 11/ no harvest	10		
SD	3	SD	3		
Minimum	8	Minimum	4		

beginning in 1950 and extending to 2135. Simulations incorporated conditions consistent with Tongass Land Management Plan alternatives 1, 9, and 11, and the pre-1954 conditions with respect to carrying capacity for deer, road construction, and exploitation of wolves and deer. Each set of simulations allowed the harvesting of wolves and then was repeated with the harvest curtailed after 1996.

Under the pre-1954 conditions, relatively large wolf and deer populations are maintained over the 200-year period (Figure 8). If wolf harvest is eliminated, a smaller deer population and larger wolf population is predicted, although deer numbers remain relatively high (Figure 9). The variability in population numbers increases if wolf harvest is curtailed, thus populations of both deer and wolves are expected to fluctuate more widely than if a harvest is maintained. It should be noted, however, that the simulated wolf harvest rate is a proportion of the wolf population and although it is allowed to vary stochastically, it generally tracks the wolf population. If trapping and hunting are less predictable and decoupled from actual wolf numbers, the effect of harvesting could be erratic and add to the variability in wolf populations rather than to dampen fluctuations.

Alternatives 1, 9, and 11 show declining wolf and deer populations (Figures 10, 11, and 12). The decline in deer numbers is exacerbated if wolf harvest is curtailed suggesting that the issue of subsistence deer hunting may become critical (Figure 13). The simulations suggest that wolf populations would likely remain well above 100 wolves after 2095 for alternative 1. Alternative 9 shows spring wolf populations below 100 wolves (on average, fall wolf populations are 25-30% larger than spring numbers) and critically low deer numbers. Simulations of alternative 11 indicate that wolf populations would number about 130 animals and the number of deer dropping to between 10,000 and 20,000 animals (depending on whether wolves are harvested). If the model predictions are

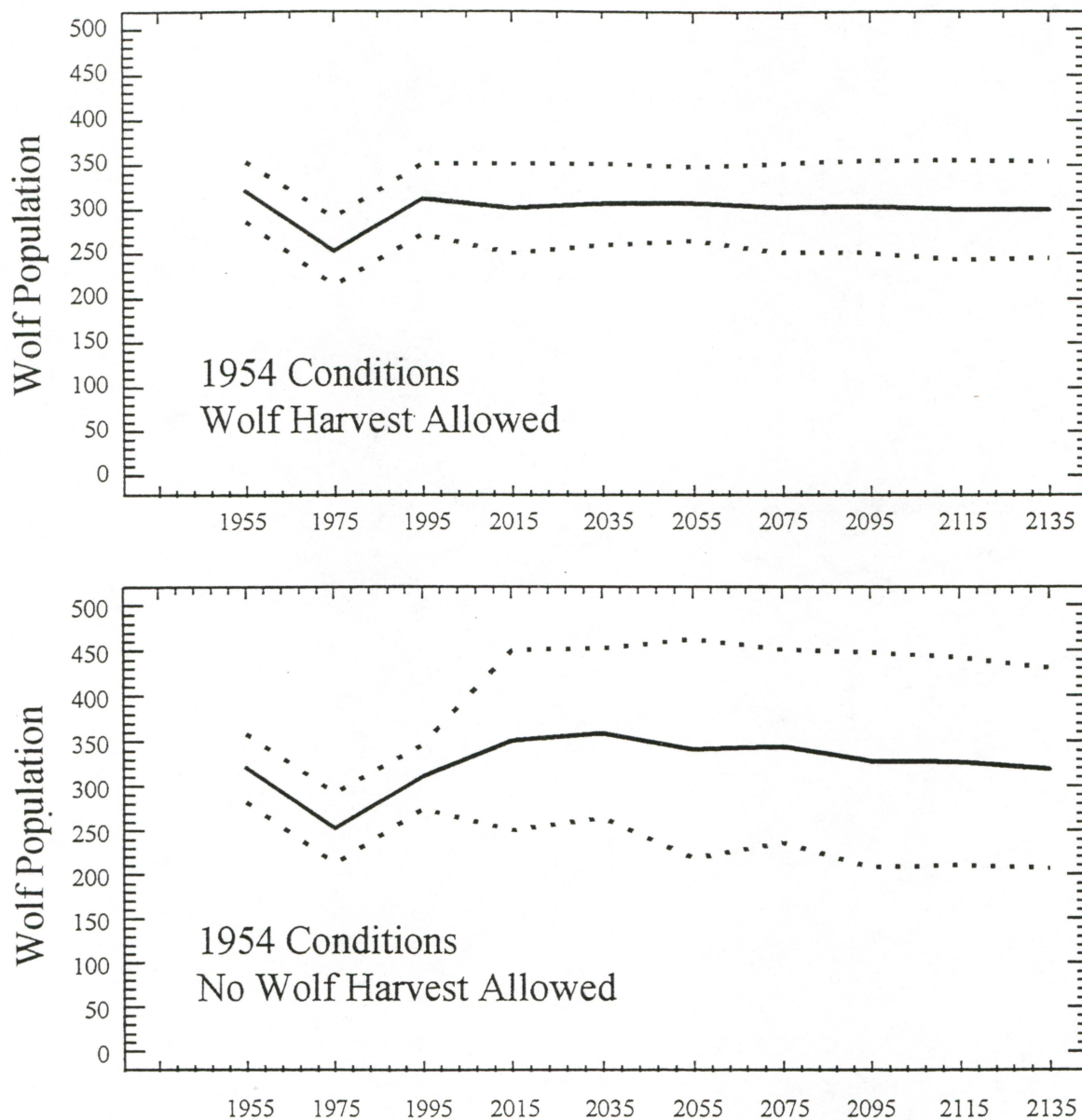


Figure 8. Graphs showing the mean prepaturient population of wolves at 20-year intervals (solid lines) and the 95% confidence intervals (dotted lines) predicted by 100 iterations of equations 3 and 10. Results shown are for the 1954 conditions. The severe winters of 1969-70 are simulated for all iterations, severe winters after 1996 are randomly spaced. The lower graph shows results when no wolf harvest is allowed after 1996.

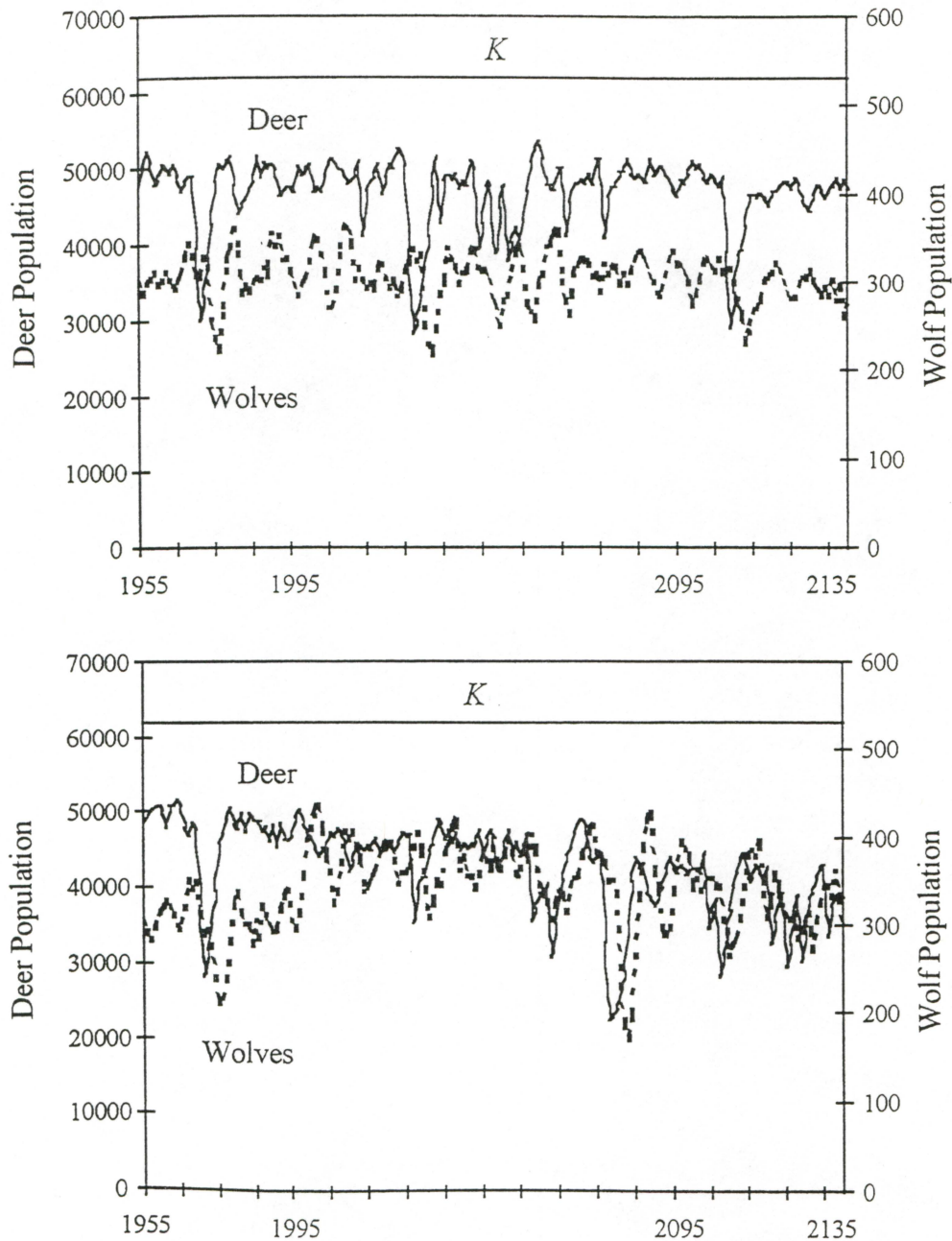


Figure 9. Graphs showing a single iteration of the wolf-deer population model (equations 3 and 10) for the 1954 conditions on Prince of Wales and Kosciusko islands. The upper graph shows the model predictions with a wolf harvest allowed. The bottom graph shows the predictions if wolf harvest is curtailed after 1996. Also shown is the effect of the severe winters of 1969-70. Winters after 1996 occur randomly with a probability of 6 per century.

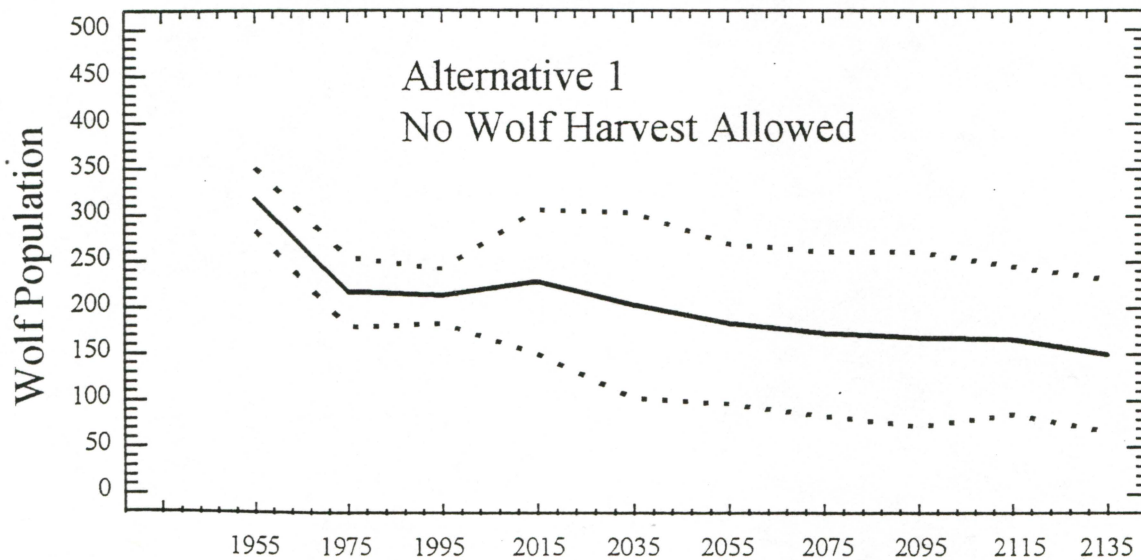
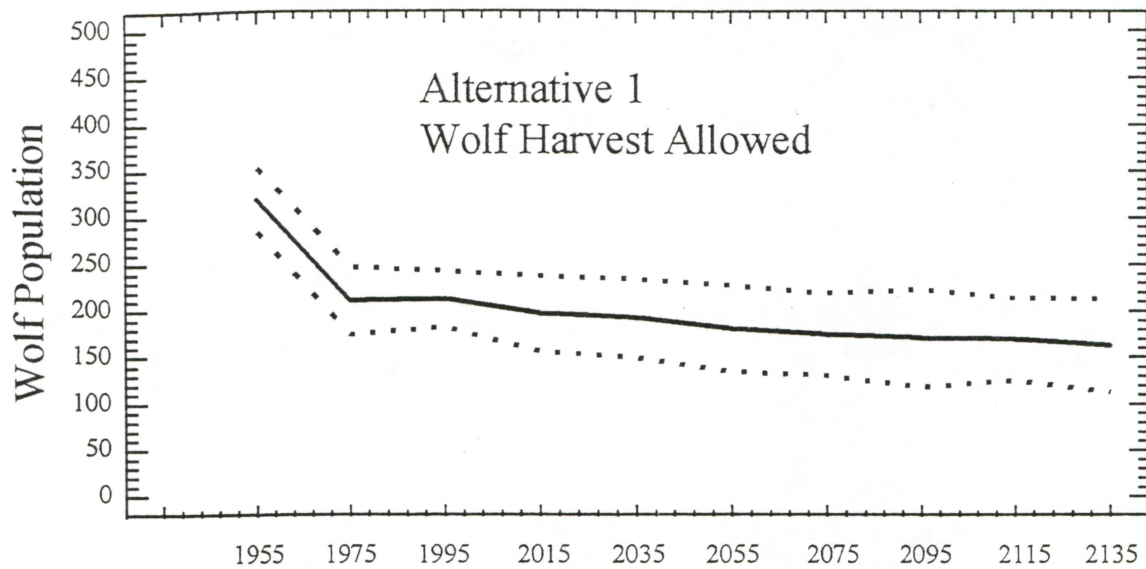


Figure 10. Graphs showing the mean prepaturient population of wolves at 20-year intervals (solid lines) and the 95% confidence intervals (dotted lines) predicted by 100 iterations of equations 3 and 10. Results shown are for Alternative 1. The severe winters of 1969-70 are simulated for all iterations, severe winters after 1996 are randomly spaced. The lower graph shows results when no wolf harvest is allowed after 1996.

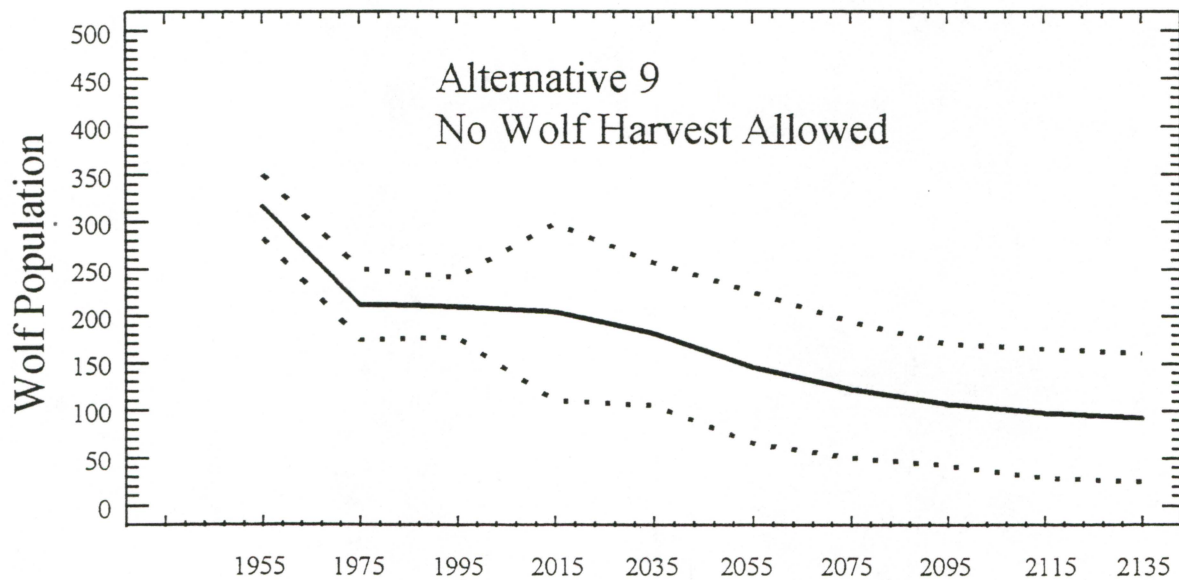
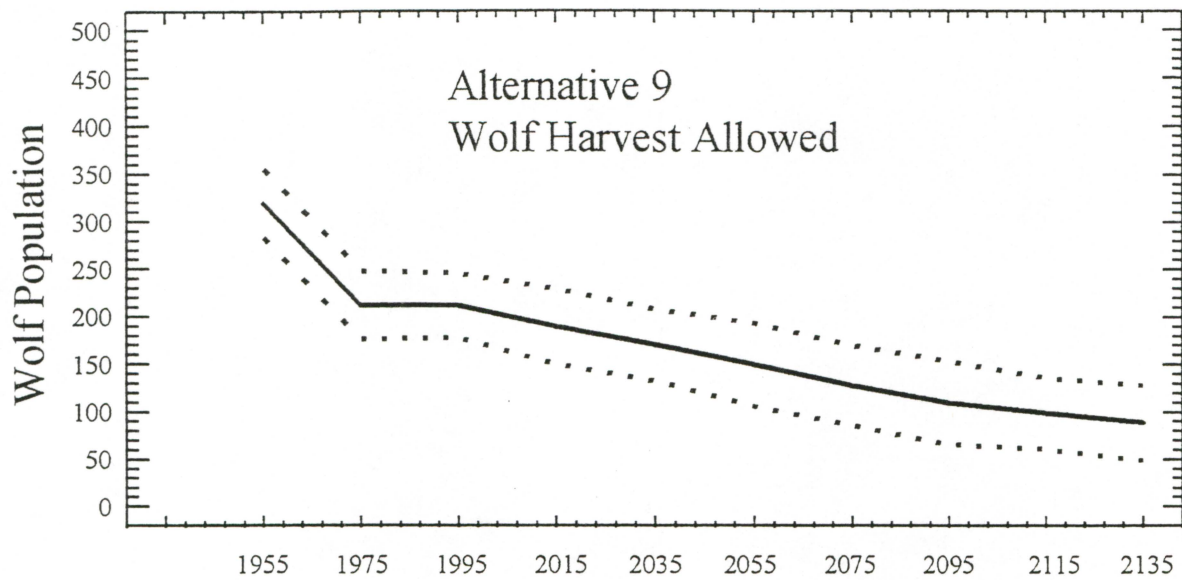


Figure 11. Graphs showing the mean prepatulant population of wolves at 20-year intervals (solid lines) and the 95% confidence intervals (dotted lines) predicted by 100 iterations of equations 3 and 10. Results shown are for Alternative 9. The severe winters of 1969-70 are simulated for all iterations, severe winters after 1996 are randomly spaced. The lower graph shows results when no wolf harvest is allowed after 1996.

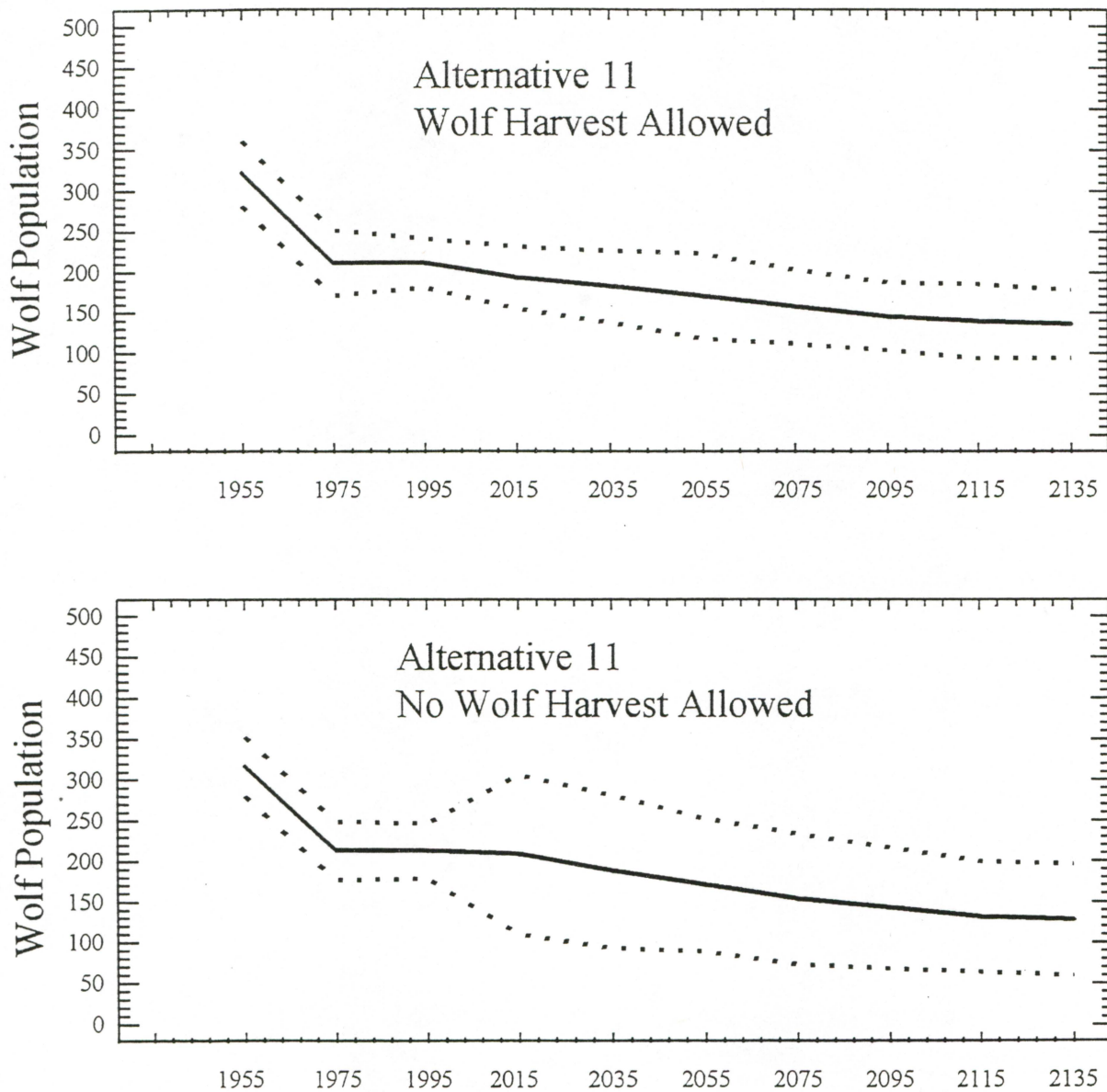


Figure 12. Graphs showing the mean prepaturient population of wolves at 20-year intervals (solid lines) and the 95% confidence intervals (dotted lines) predicted by 100 iterations of equations 3 and 10. Results shown are for Alternative 11. The severe winters of 1969-70 are simulated for all iterations, severe winters after 1996 are randomly spaced. The lower graph shows results when no wolf harvest is allowed after 1996.

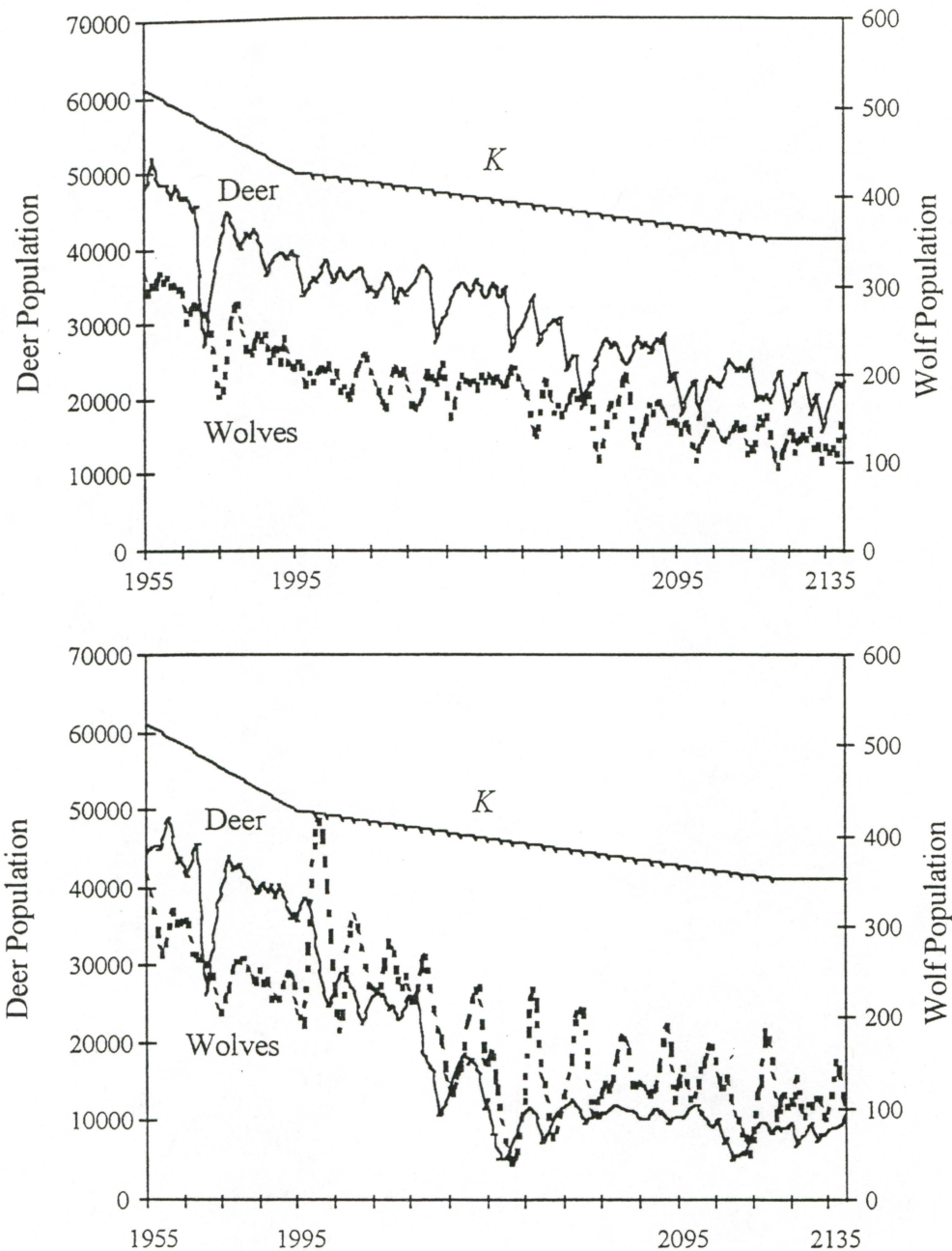


Figure 13. Graphs showing a single iteration of the wolf-deer population model (equations 3 and 10) for TLMP alternative 11 on Prince of Wales and Kosciusko islands. The upper graph shows the model predictions with a wolf harvest allowed. The bottom graph shows the predictions if wolf harvest is curtailed after 1996. Also shown is the effect of the severe winters of 1969-70. Winters after 1996 occur randomly with a probability of 6 per century.

accurate, deer populations will decline disproportionately to the decay in carrying capacity and subsistence hunting for deer may be in jeopardy by the middle of the next century.

We conducted simulations of the model with the conditions for alternatives 1 and 11 in 2135 kept constant for 100 years to assess the risk of extinction for wolves at population levels predicted at the end of the TLMP planning period. We also simulated wolf and deer populations with the 1954 conditions held constant as a control. We modeled winters and harvested and unharvested wolf populations for each scenario (Table 5). None of the simulated populations went extinct for either alternative, although a number of the iterations of the model showed minimum populations that were ≤ 30 wolves. The results suggest that the median preparturient wolf population after 2135 would likely hover near 180 wolves for alternative 1 and 130 wolves for alternative 11. Unharvested populations of wolves were generally lower than harvested populations because of greater probability that deer numbers were suppressed following severe weather conditions. In contrast, for the 1954 conditions, harvested wolf populations were consistently lower than unharvested populations indicating that carrying capacity was sufficiently high under pristine conditions to enable deer to rapidly bounce back after severe winters. The mean wolf populations at 10-year intervals had smaller variances when wolf harvest was allowed than when harvest was curtailed. In addition, the minimum populations were generally larger as well (Table 5). This is consistent with the previous simulations and suggests that wolf harvests that track wolf population levels may dampen population fluctuations. We reiterate, however, that wolf harvests that vary independently of wolf populations will exacerbate annual variability in wolf numbers.

Table 5. Results of Monte Carlo simulations ($n = 100$) of the wolf-deer model showing the median spring preparturient deer and wolf populations for each decade after 2135. The scenarios for the 1954 conditions and alternatives 1 and 11 were simulated with and without a wolf harvest; winters were simulated for both scenarios. Shown are the median and minimum populations by decade.

Wolf Populations										
Decades After 2135										
	1	2	3	4	5	6	7	8	9	10
1954 Conditions/ wolf harvest	302	309	308	308	305	305	302	307	308	303
Minimum Pop.	207	243	214	246	217	196	192	207	94	112
1954 Conditions/ no harvest	366	371	367	363	361	360	340	339	341	337
Minimum Pop.	223	177	102	140	136	179	177	136	102	159
Alternative 1/ wolf harvest	195	194	136	184	180	177	174	174	172	169
Minimum Pop.	103	137	76	98	130	106	110	88	74	99
Alternative 1/ no harvest	216	214	194	181	180	171	175	171	165	164
Minimum Pop.	25	79	90	87	75	66	60	48	73	86
Alternative 11/ wolf harvest	137	136	137	129	133	131	128	129	127	123
Minimum Pop.	80	81	77	51	78	62	69	41	54	70
Alternative 11/ no harvest	124	120	116	121	117	113	118	120	108	107
Minimum Pop.	54	43	26	34	50	30	9	47	44	43

The frequency that simulated wolf populations dropped below 100 animals at least once during a 100-year period following 2135 increased significantly for alternatives 1 and 11 when compared to the 1954 conditions (Tables 6 and 7). When wolves were not harvested, populations were 103 and 2,376 times more likely to drop below 100 animals for alternatives 1 and 11, respectively. Harvested populations were 8.6 and 193 times more likely to drop below 100 wolves for alternatives 1 and 11 than under the 1954 conditions. Alternative 11 increased the risk of populations dropping below 100 wolves by a factor of 21 for unharvested populations and by a factor of 11 for harvested populations when compared to alternative 1 (Tables 6 and 7). In addition, 69% of the iterations of the model predicted that wolf numbers would drop below 75 animals for alternative 11 when wolves are not harvested and 10% of the iterations showed numbers of wolves dipping below 75 animals when they are harvested (Tables 6 and 7). These results suggest that although the median and mean populations of wolves on Prince of Wales and Kosciusko islands will likely be above 100 animals after 2135, there is a significant risk that the preparturient number of wolves will periodically drop below 75-100 animals.

DISCUSSION AND CONCLUSIONS

Predictions from the wolf-deer model suggest that alternatives 1 and 11 of the revised Tongass Land Management Plan probably do not threaten wolves on Prince of Wales and Kosciusko islands with extinction in the next century unless a catastrophic event such as a disease outbreak occurs (canine parvovirus has been reported recently in the vicinity of the town of Craig on Prince of Wales Island). All of the results from the models consistently predict preparturient wolf populations >100 animals except those for alternative 9. Nonetheless, wolf numbers will decline perhaps as much as 30-40% by 2135

Table 6. Frequency that wolf populations predicted by the wolf-deer population model drop below 100 and 75 animals at least once during a 100-year period after 2135. Shown are comparisons between the 1954 conditions, alternative 1, and alternative 11 for wolf populations that are not harvested. Also shown are the odds ratios for each comparison.¹

	<u>1954</u>	<u>Alt. 1</u>
<100	1	51
≥100	99	49

$\chi^2 = 65.5$ $P = 0.000^*$
Odds Ratio = 103

	<u>1954</u>	<u>Alt. 1</u>
<75	0	24
≥75	100	76

$\chi^2 = 24.4$ $P = 0.000^*$
Odds Ratio = 64

	<u>1954</u>	<u>Alt. 11</u>
<100	1	96
≥100	99	4

$\chi^2 = 180.6$ $P = 0.000^*$
Odds Ratio = 2,376

	<u>1954</u>	<u>Alt. 11</u>
<75	0	69
≥75	100	31

$\chi^2 = 101.6$ $P = 0.000^*$
Odds Ratio = 443

	<u>Alt. 1</u>	<u>Alt. 11</u>
<100	51	96
≥100	49	4

$\chi^2 = 52.0$ $P = 0.000^*$
Odds Ratio = 21

	<u>Alt. 1</u>	<u>Alt. 11</u>
<75	24	69
≥75	76	31

$\chi^2 = 40.7$ $P = 0.000^*$
Odds Ratio = 7

* Significant at $\alpha \leq 0.05$ after controlling for comparison-wise error rate.

¹ To approximate the odds ratio when one or more cells are zero, 0.5 is added to each cell.

Table 7. Frequency that wolf populations predicted by the wolf-deer population model drop below 100 and 75 animals at least once during a 100-year period after 2135. Shown are comparisons between the 1954 conditions, alternative 1, and alternative 11 for wolf populations that are harvested. Also shown are the odds ratios for each comparison.¹

	1954	Alt. 1		1954	Alt. 1
<100	0	8	<75	0	1
≥100	100	92	≥75	100	99
$\chi^2 = 5.7$ $P = 0.017^*$			$\chi^2 = 1.0$ $P = 0.316$		
Odds Ratio = 8.6			Odds Ratio = NA		
	1954	Alt. 11		1954	Alt. 11
<100	0	49	<75	0	10
≥100	100	51	≥75	100	90
$\chi^2 = 61.4$ $P = 0.000^*$			$\chi^2 = 7.8$ $P = 0.005^*$		
Odds Ratio = 193			Odds Ratio = 23		
	Alt. 1	Alt. 11		Alt. 1	Alt. 11
<100	8	49	<75	1	10
≥100	92	51	≥75	99	90
$\chi^2 = 41.2$ $P = 0.000^*$			$\chi^2 = 7.8$ $P = 0.005^*$		
Odds Ratio = 11			Odds Ratio = 11		

* Significant at $\alpha \leq 0.05$ after controlling for comparison-wise error rate.

¹ To approximate the odds ratio when one or more cells are zero, 0.5 is added to each cell.

as a result of the loss of deer carrying capacity expected under alternative 11. An extension of the current conditions (alternative 1) indicates a decline of 20-30% and alternative 9 would result in a 50-60% reduction in wolf numbers.

Simulations suggest that the historical (pre-1954) spring wolf population likely was about 300-320 animals for Prince of Wales and Kosciusko islands. Therefore, the wolf populations predicted for alternatives 1, 9, and 11 represent reductions of 45-55%, 65-75%, and 55-65% from historical levels, respectively. The prediction that wolf populations will remain above 100 animals after 2135 assumes no further decay in carrying capacity for deer. Further, our analyses do not account for the genetic consequences for a declining wolf population.

The model simulations generally represent optimistic conditions. The predator-prey model assumes that 1) all pack areas have equal chances of recolonization regardless of their geographic position; 2) as long as the pool of dispersers is greater than the demand for immigrants, successful recolonization of a vacant pack area is guaranteed; and 3) wolves are assumed to have priority in acquiring prey and humans are allocated the residual deer. This last assumption is problematical. As deer numbers decline there will probably be competition between wolves and subsistence hunters for deer. The consequences for wolves are difficult to predict but it is likely that management agencies will be pressured by subsistence users to control wolf numbers. The effects of intensive management of wolves on the risk of local extinction was not considered in our simulations.

The population modeling assumes that deer habitat capability values are reasonable predictions of the future carrying capacity for deer. Although our simulations indicated a low probability of extinction for wolves over the next century, the margin of error is small with respect to the minimum viable population of 100 wolves suggested by the U. S. Fish

and Wildlife Service for each subgroup of a metapopulation (of course this assumes that wolves on Prince of Wales and Kosciusko Islands are linked to other wolf subpopulations in southeastern Alaska; an untested hypothesis). If the predictions for K are as little as 10% too high, the risk of the wolf population dropping below 100 animals in spring increases negligibly for unharvested populations but increases 4-fold for harvested populations (Figure 14). In addition, simulations show a four-fold increase in the number of wolf populations dropping below 50 animals in spring (Figure 14). Clearly, it is important to validate the deer habitat capability model by independent means and to devise other methods to estimate deer numbers or carrying capacity.

In summary, we conclude:

1. It is unlikely that TLMP alternatives 1 or 11 would result in the extinction of wolves from Prince of Wales and Kosciusko islands in the next century. Alternative 9 would probably result in wolf populations low enough to be of questionable viability with respect to demographic parameters (as opposed to genetic ones).
2. The wolf population on Prince of Wales and Kosciusko islands will probably decline by 30-40% as a result of alternative 11 and 50-60% as a result of alternative 9. If current habitat conditions are maintained (alternative 1) wolf numbers may still decline 20-30% by the end of next century.
3. Carrying capacity for deer was sufficiently high prior to 1954 to enable deer populations to rebound from severe winters in the face of wolf predation and hunting by humans. This is a reasonable conclusion considering that wolves and deer likely have persisted on Prince of Wales Island for centuries. Current habitat conditions may not be adequate to prevent long periods in which deer numbers are suppressed by wolf predation

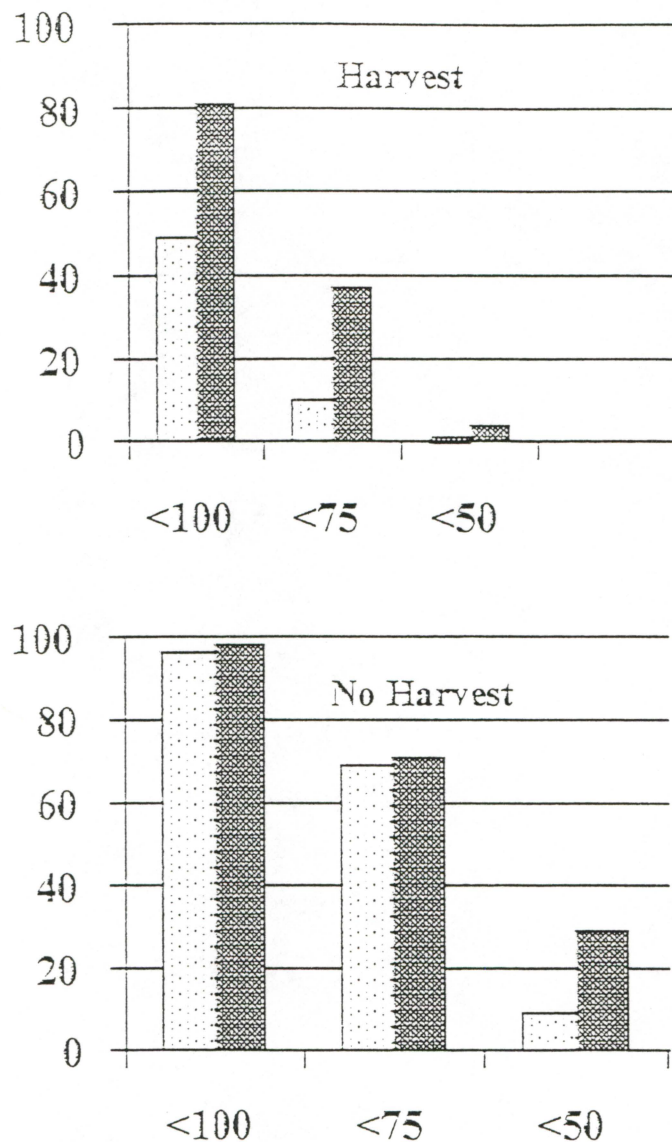


Figure 14. Histograms showing the percent of wolf populations predicted by the wolf-deer model that drop below 100, 75, and 50 animals at least once in a 100-year period. Light bars show results for Alternative 11 and dark bars show results for Alternative 11 if deer habitat capability values overestimate K by 10%. The histograms show the sensitivity of the model to values of K and underscores the importance of reliable estimates of carrying capacity.

following severe winters. This situation will worsen as carrying capacity for deer continues to decay as a result of alternatives 9, and 11.

4. It may be very difficult to maintain wolf numbers and simultaneously meet the demand for deer by subsistence hunters next century because of chronically low deer populations resulting from the loss of carrying capacity.

ACKNOWLEDGMENTS

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APPENDIX 1

Comparison of Pellet-Group Surveys and USFS Deer Habitat Capability

The main concern for the conservation of wolves that was emphasized in the wolf conservation assessment (Person et al. 1996) was the effect that timber harvesting would have on deer populations. Currently in southeastern Alaska there are only two sources of information on deer abundance, pellet-group surveys and deer harvest statistics. There is only one mechanism in place to monitor the effects of timber harvest on deer, the USFS HSI model for deer.

Deer harvest statistics are of questionable value in tracking deer population levels. Certainly, as deer populations change, the number of deer harvested will change as well; however the relation may not be evident until large changes in deer density occur. In addition, deer harvest is strongly linked with human access. For example, in GMUs 2 and 3, the reported average deer harvest by WAA between 1990-1995 is correlated ($r = 0.81$) with the linear kilometers of road within WAAs. Current harvest numbers may not reflect deer populations in GMUs 2 and 3 at all.

Pellet-group (PG) surveys are the only extensive method used to monitor deer population trends in southeastern Alaska. PG surveys have the advantage in that they directly measure deer activity along a specified transect. Nonetheless, PG survey data suffer from large variances from year to year and are relatively insensitive indicators of deer population trends. Further, conversion of PG data to estimates of deer density are imprecise. Seasonal variability in defecation rates, persistence of pellets, errors in identifying and counting groups combine to confound simple relations between pellet group density and actual deer numbers. Further, pellet-groups represent the cumulative

activity of deer in an area and density of deer estimates based on PG surveys will likely overestimate the actual number of deer.

The USFS deer habitat capability model is a tool used to compare the effects of various timber harvesting plans on carrying capacity for deer. It is based on the collective wisdom of a group of wildlife biologists knowledgeable about deer in southeastern Alaska. Presumably it reflects the habitat preferences of deer and the importance of winter habitat. Unfortunately, the model has been frequently revised on the basis of "professional judgment" rather than empirical data. The model has not been adequately validated (if in fact it can be validated) and has undergone little review. It was designed as an index; however, it is currently being used to predict actual deer numbers in order to evaluate whether various timber harvest alternatives meet the recommendations of the wolf conservation assessment (Person et al. 1996). Thus it is being used for a job for which it was never intended.

It should be clear that no adequate monitoring systems are in place to estimate current deer populations or to track future changes with reasonable accuracy and precision. At the very least it would be valuable to know if deer HSI is correlated with the pellet group data. If the relation were strong then the HSI model could be relied on to provide some information about real deer numbers.

In collaboration with Matt Kirchhoff of the Alaska Department of Fish and Game, we compiled ADF&G pellet survey data between 1988-1996 for 30 U. S. Forest Service Value Comparison Units (VCU; each VCU approximately represents a watershed) in the northern portion of the Alexander Archipelago. We chose areas without wolves to eliminate the confounding influence of predation on the number of pellet groups observed. Data were tabulated for 95 transects over 7 years for a total of 262 transect-years

involving 19,637 plots. The VCUs sampled were located on Admiralty, Baranof, and Chichagof islands and generally were surveyed for an average of 3 years. We calculated the HSI value for each transect and the average number of pellet groups per plot across years for each transect. Pellet group numbers were adjusted for undercount bias by multiplying the count by 1.13 for plots under open canopies and 1.40 for plots under closed forest canopies (Kirchhoff 1990). We compared the HSI values with the average number of pellet groups (Figure A1). It was clear that 3 transects (VCU 247 Trans #2[Finger Mountain], VCU 296 Trans 5, and VCU 298 Trans 2) had extremely high pellet counts that were well beyond the 95% confidence limits for the mean of all transects (Figure A2). We considered these values to be outliers and deleted them from the rest of the analysis. After eliminating outliers, we regressed HSI values against the mean number of pellet groups. The pellet group data for each transect were weighted by the number of years the transect was surveyed because we felt data from transects sampled over many years provided a better estimate of annual variation and were more reliable indicators of deer density. Results from the regression analysis indicate that HSI is significantly correlated with the mean number of pellet groups per plot but the r^2 value is very low, suggesting that HSI is a poor predictor of deer activity (Table A1).

The deer density predicted for an HSI value of 1 is 98 deer per mile² with the 90% lower bound at 84 deer per mile² and the 90% upper bound at 118 deer per mile². The current HSI model assumes a density of 125 deer per mile² for an HSI of 1. Based on our analysis, we suggest that 100 deer per mile² is a more appropriate value. This estimate should be considered as a maximum value because pellet-groups represent the cumulative activity of deer over time and density estimates derived from them will likely overestimate the number of deer. Only one severe winter (1990-1991) that resulted in deer mortality occurred during the period that pellet group data were collected and the effects were localized (Kirchhoff *pers comm.*). Deer numbers were likely close to a sustainable

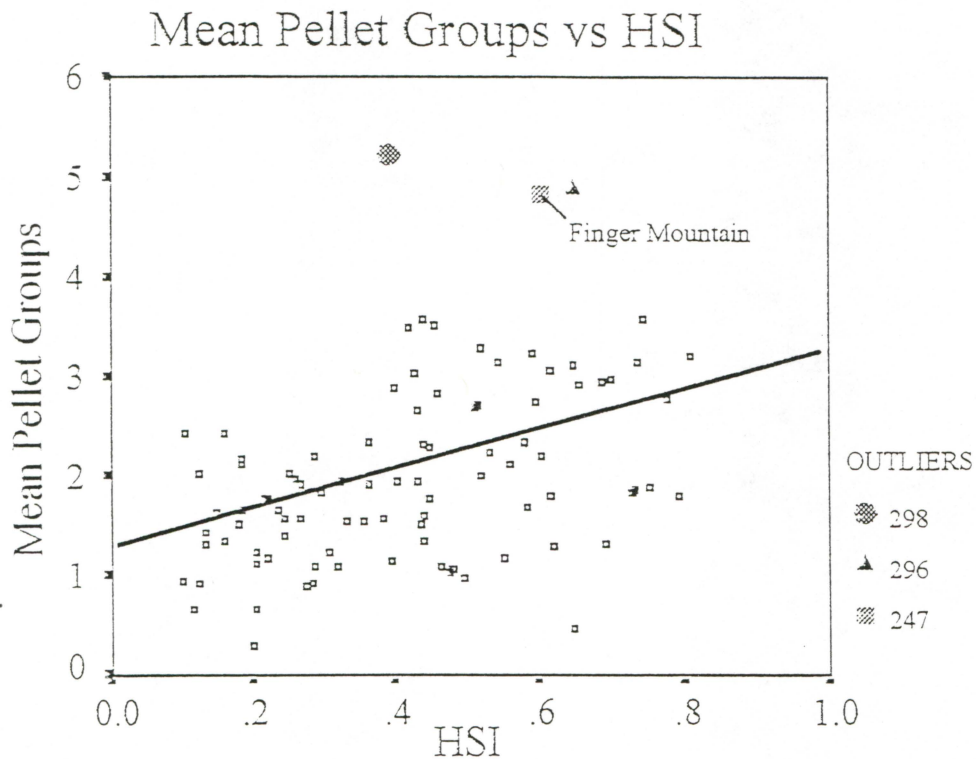


Figure A1. Weighted regression of mean number of pellet groups per plot along individual transects versus the HSI score for the transect. The outliers are individual transects within VCUs 247, 296, and 298 that had anomalously high pellet-group counts that were beyond the 95% confidence limits for the data from all of the transects.

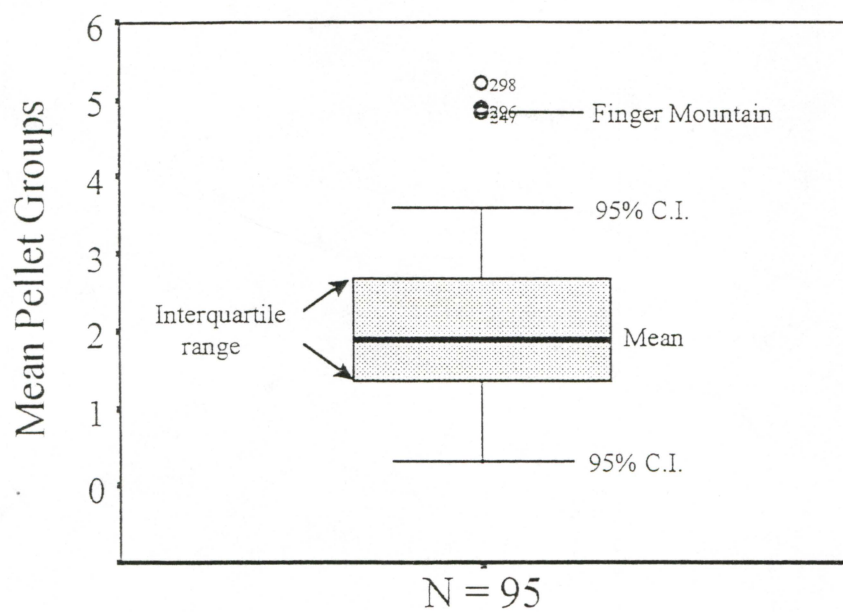


Figure A2. Box and whisker plot of mean number of pellet groups per plot along individual transects. The outliers shown represent data from transects in VCUs 247, 296, and 298.

carrying capacity and the pellet group data probably represent the best empirical measure of that carrying capacity available at this time. Therefore, the current deer HSI numbers provided by the Forest Service should be reduced by 20% (100/125). For HSI values that were reduced to account for wolf predation (predicted habitat capability for deer is actually 36% higher) the numbers should be multiplied by 1.09 (1.36×0.8). It is important to understand that these estimates represent carrying capacity. For a deer population to produce about 30% fawns annually (as assumed in the equilibrium model described in the wolf conservation assessment) the actual deer population should be about 70% of K. Thus the recommendation of 13 deer per mile² given in the wolf conservation assessment corresponds to a K of 18 deer per mile² (note that this is a revision of our original report and is the result of a more rigorous analysis).

Although our analysis may improve the evaluation of data currently available on deer numbers, it underscores the enormous uncertainty surrounding deer populations and any predictions for the future. Hopefully, some credible plans will be forthcoming from either the USFS or ADF&G to improve the database and adequately track the effects of timber harvest.

Table A1. Results of regression analysis of deer HSI against the mean number of pellet groups per plot for 92 transects in 30 VCU's located in southeastern Alaska.

Model:

Mean Number of Pellet Groups = $1.19 + 1.88 (\text{HSI})$ $r = 0.47, P = 0.000$

β_0 : 1.19, $t = 7.0, P = 0.000$; β_1 : 1.88, $t = 5.1, P = 0.000$; $r^2 = 0.22$

For HSI = 1: Mean # Pellet Groups = 3.07 or 98 deer/mile²

90% lower bound = 84 deer/mile²

90% upper bound = 118 deer/mile²

OPTIONAL FORM 99 (7-90)

FAX TRANSMITTAL

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To TON NICKLES	From ED GROSSMAN
Dept./Agency RO	Phone #
Fax #	Fax #

NSN 7540-01-317-7368

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GENERAL SERVICES ADMINISTRATION

November 14, 1994

Memorandum

To: Wolf file

From: Assistant Endangered Species Specialist *Ed Grossman*Subject: Phone conversation with Dave Person, wolf researcher
Prince of Wales Island

I received a copy of Dave's October 26, 1994 letter to Dave Rittenhouse, USFS Ketchikan Area supervisor. On page three Dave reiterated some of the problems associated with the USFWS news coverage of his work this summer. I called Dave to update him on the latest news regarding joint public outreach efforts in Southeast Alaska. I also asked if there were anything else we could do in the interim to take some of the heat off of him. He appreciated the offer, but said things have cooled down a bit recently and that the outreach efforts in progress should be enough for now.

I also asked Dave about his statement that wolves are not endangered on Prince of Wales since he has been indicating they have less than a bright future based on his work and observations to date. He clarified that the statement was in the context of the Endangered Species Act, and that although he did not think the wolf was in immediate risk of endangerment, he predicated a very real problem in the future or in other words they may be threatened. He indicated that for numerous areas on POW it is likely too late for deer and thus wolves. He used the Control Lake and Staney Creek areas as an example indicating that the remaining old growth, which is less than high volume, is in strips and is at too high an elevation to be effective critical deer winter habitat. Dave predicted that one or a series of bad winters will likely cause a dramatic decline in deer numbers, and it may be that they remain depressed. He noted that this may be the year saying that winter has arrived on POW already, where as it did not show up in force last year until February.

David K. Person
P.O. Box 896
Craig, AK 99921
(907) 530-7042

26 October 1994

David Rittenhouse
Supervisor, Ketchikan Area
USDA Forest Service
Tongass National Forest
Ketchikan, AK

NOV 9 1994

Dear Dave,

I'm sorry that I haven't written to you in so long. I had a recent conversation with Cole Crocker-Bedford and he mentioned that you were asking about how we were doing on the wolf project. I am going to write a progress report in mid-November, however, I thought that you might appreciate an update before then.

Since the beginning of the project we have radio-collared 24 wolves (11 adults, 7 yearlings, and 6 juveniles). Unfortunately, 8 wolves were killed by trapping or shooting, one died from unknown causes, one was probably killed by a bear, and one had the collar chewed off its neck. Two other wolves were trapped but released unharmed. I estimated survivorship to be only 39% ($\pm 22\%$, $n = 19$) for wolves monitored between June 1, 1993 and June 1, 1994 using a Kaplan-Meier staggered entry procedure. Most of the study animals that were killed were trapped, shot, or snared along the road system. The upper 95% confidence band for survivorship is 61%, which still implies a 39% mortality rate. If this is representative of the population then there will likely be a decline in wolves in the north and central portions of Prince of Wales Island.

To date we have managed to collect approximately 1,000 radio-locations, most recorded from the ground. About 20% of the radio-relocations are nighttime observations giving us data with respect to daily activity patterns. Home ranges for 11 wolves are mostly between 200-400 km², although some are over 400 km². These estimates are larger than those reported in my progress report of November 1993, and reflect the addition of winter and spring data. I will be refining the estimates for my next progress report by subjecting them to systematic outlier analyses, and then will compare home ranges by landscape type.

We were able to locate and measure two more dens this spring. Both had similar characteristics: excavated in root wads of large trees, adjacent to fresh water, and facing more or less east or southeast. All dens that we have measured to date ($n = 7$) were located in old-growth patches near muskegs, lakes, or streams, however, several have been within 200m of actively used roads.

We have not analyzed the ground-based telemetry data for habitat use, however, 168 (94%) out of 179 aerial relocations recorded between March 1993 and October 1994 were of wolves in old growth (high and low volume) or muskeg. These data include wolves occupying predominantly logged

landscapes as well as those in relatively undisturbed areas. The observations represent micro-habitat selection during daytime. We still have not looked at our nighttime data nor have we examined selection at the landscape level.

Habitat selection by wolves is probably a function of security (particularly during denning periods), shelter from weather, and the availability of prey. The last factor is likely to be the most important, and emphasizes the need to know much more about the interactions of deer, wolves, and habitat. For instance, are wolves resting in old-growth patches during the day and hunting along roads or in second growth during the night? Our nighttime telemetry data will shed some light on this because it is a well supported assumption that when wolves are moving they are probably hunting. The alternative is that they seek most of their prey in old growth or muskegs and avoid second growth entirely. If the latter is the case, will extensive timber harvesting concentrate deer (especially in winter) in remnant uncut patches and increase predation efficiency? Will this destabilize predator-prey dynamics? Unfortunately, comprehensive examination of these questions is beyond the scope of my present work and will require much more time, money, and effort.

Twelve of our 24 wolves have exhibited dispersal behavior. Two of the three study animals on Kosciusko Island migrated all the way to the southern portions of Prince of Wales and Dall Islands. One of these animals has joined a pack of 12 wolves near Cholmondeley; the other is alone on the south end of Dall Island. It was a rather poignant experience for me to have had the chance to see this last animal as an active pack member last year on Kosciusko Island, and now to see him curled up alone on a ridge top overlooking desolate and forbidding Cape Muzon. The dispersal rate is remarkable because over half of the dispersers are adults. Generally, dispersal behavior will increase when wolf density is low and prey biomass is high, inducing wolves to seek breeding opportunities in vacant territories. Nonetheless, if wolf density is high with respect to prey biomass, animals may be forced to leave pack territories because the area can no longer support them. Several studies have shown, however, that starvation conditions must be reached before wolves disperse due to limited food. A predominance of adult dispersers may be expected under the first scenario as older, more aggressive (and previously sexually suppressed) individuals strike out on their own. Younger dispersers might be expected in the second scenario because they would be the least able pack members to compete for limited food. I suspect that the high harvests of wolves over the last three years have reduced populations in the northern portion of POW and this may explain the dispersal rate.

Reliable estimates of absolute deer density would be very valuable to understanding predator-prey dynamics on POW Island. Although my present work only requires that I crudely estimate relative prey density with respect to wolf territory size and habitat composition, I am interested in developing techniques that will yield precise estimates. I have made contact with an engineer from the Air Force office of technology transfer at Wright AFB in Ohio who is interested in our work. He is checking on the suitability of some of their military aerial infrared censusing capability for estimating deer numbers under southeast Alaskan conditions. If the technology looks promising, I will pursue a grant from the Department of Defense to fund an experiment in southeast Alaska. I will keep you informed about my progress.

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As you can well imagine, the petition to list the wolf has made our lives and work difficult, to say the least. The television coverage arranged by the Fish and Wildlife Service did not help considering the slant taken by the reporter that easily led to a perception that we were working for the Fish and Wildlife Service on research inspired by the petition. Contrary to the implications drawn from the TV spot, wolves are not endangered on POW Island. Because we are the only ones doing research with wolves in southeast, we have been bombarded with information requests since the petition was filed. It would be nice if FWS, ADF&G, or the Forest Service would provide the public with some basic information about wolves, our research, and perhaps the petition. As I told Larry Meshew when he visited us last summer, I would rather not have to run a PR campaign and mediate between the public, USFS, FWS, and ADF&G. However, because of all the hype about wolves and goshawks, we have definitely become a local target. I'm sure the misinformation that abounds in the press is partly responsible for one of our trapped wolves being shot before we could collar the animal. The person or persons involved were driving along a road closed to motorized vehicles when they spotted the wolf. They shot it in the neck and threw it and the trap over an embankment.

We are finally making some progress on the genetic portion of my work. Dr. Gerry Shields is running samples in his lab at UAF. We received funding from the USFS regional office, FWS, and ADF&G to do the preliminary work. Gerry and I will probably have some results by April 1995. I may spend a short period this winter in Fairbanks working with Gerry. It is very exciting to get this work going and to have Gerry running the samples. He is one of the most experienced and skilled practitioners of mtDNA analysis with respect to studies of avian and mammalian evolution. Our work should shed some light on the origin and population structure of Archipelago wolves. Unfortunately, most people are interested in the subspecific status of the wolf, a question in which I really have no interest. Whether we call it Canis lupus ligoni or Canis lupus nubilus is not important. These names are simply scientific labels. What is important is whether or not Archipelago wolves are a genetic group distinct from other Alaskan or Canadian populations and whether or not there is one regional Archipelago wolf population or are there many small separate populations associated with the major islands and the mainland. Our efforts to understand the ecology and genetics of southeast Alaskan wolves will ultimately illustrate why I believe that these animals are one of the most scientifically important group of wolves in the world. We may have 20 or more Isle Royales in our midst.

About a month ago, I had a good conversation with Anne Archie about the wolf project. I told her that I was very interested in pursuing future research concerning the interactions of wolves, deer, and their habitat, as well as how to manipulate second growth to benefit both species. Regardless of what happens because of the petitions, PACFISH, or the new Tongass plan, the majority of high-volume forest on POW will be cut. Unless the biologists are wrong about the dependence of deer on high-volume stands for wintering habitat (or global warming accelerates and we end up with a climate like southern California), deer are going to decline. It's analogous to having a fishbowl full to the brim with fish; you remove 30% of the water and you're not going to have as many fish. The consequences for wolves, subsistence, and sport hunting could be complicated and unpleasant. I described to Anne an idea that I have to establish 4 long-term study sites, one logged with no alpine terrain, one logged with alpine terrain, one unlogged with no alpine,

and one unlogged with alpine habitat. The alpine zones are the result of vertical heterogeneity which may play an important role particularly if the quality of summer and fall deer range is as important as winter habitat. We would radio-collar both deer and wolves and observe mortality rates, predation patterns and habitat use. After describing current characteristics of wolf-deer interactions, we would then manipulate the previously logged habitat by clearcutting and thinning second growth to create between-stand heterogeneity (if it is possible). Treatments would be made to both young and old second growth to try and enhance deer habitat at a landscape level (as opposed to concentrating efforts on a micro-habitat scale). I envision such a project as involving both the Thorne Bay and Craig districts with a team of biologists, foresters, and ecologists involved. Furthermore, once the project infrastructure was established, numerous other research projects could be piggybacked with it that would expand the work to include other animals and plants, and possibly whole ecological communities. Anne was interested in my ideas and suggested that I mention them to you. I haven't had the time to develop them further, however, I wanted to see if you or your staff were interested in this kind of project. It could be a way to coordinate a number of research efforts towards a common goal - maintaining viable ecological communities after logging. I would certainly appreciate any thoughts that you have concerning this.

Finally, I wanted to thank your staff and the Thorne Bay and Craig districts for their continued support of my work. They always seem to be there when I need them. I also wanted to invite you to visit us at your convenience. I enjoyed your last visit and look forward to a future one. Moira and I don't need much warning and can work around your schedule. Again, thank you for your support and don't hesitate to contact us if you have any questions or concerns about what we are doing.

Sincerely,



David K. Person

cc: A. Archie
C. Crocker-Bedford

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