ECOLOGY OF THE ALEXANDER ARCHIPELAGO WOLF
AND RESPONSES TO HABITAT CHANGE

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The topography of southeastern Alaska was molded by the interaction of tectonic forces with glacial activity (Klein 1965), resulting in a mountainous, glaciated strip of mainland and an archipelago of rugged islands (Fig. 1). Although ice-free refugia probably existed (Baichtal pers. comm.), current plant and animal communities occurring in the region evolved during the 10,000-year period since the last major glaciation. Numerous plant and animal species colonized southeastern Alaska from the south via the coast of British Columbia (Klein 1965). One potential southern immigrant is the gray wolf (Canis lupus), which may have followed Sitka black-tailed deer (Odocoileus hemionus sitkensis) north from Washington and southern British Columbia (Klein 1965, Friis 1985). Morphological evidence from skulls strongly suggests a southern connection for wolves in southeastern Alaska (Nowak 1983, Friis 1985, Nowak 1994) (Fig. 2).

Separated from interior mainland areas by the glaciated Coast Mountains, wolves in southeastern Alaska are distinct from other Alaskan and British Columbian wolf populations (Pedersen 1982, Nowak 1983, Friis 1985, Nowak 1994). Similar in appearance to the original Vancouver Island wolf (C. l. crassodon), southeastern Alaskan wolves tend to be darker and shorter-haired than wolves in other portions of Alaska, with a black color phase making up 20 to 50% of the annual wolf harvest. They tend to be smaller than other Alaskan wolves, with adult males averaging 39.5 kg and females averaging about 7 kg less (Wood 1990). Adult male wolves captured on Prince of Wales Island as part of this study, however, averaged only 34.5 kg and females averaged 33.6 kg, and only 14.5% of the wolves harvested over the last three years in the same area were black.

Based on skull morphology, Goldman (1944) deemed wolves in southeastern Alaska to be sufficiently distinct to warrant their own subspecific classification. He gave the name Canis lupus ligoni to the population, which later became known as the Alexander Archipelago wolf. The range of the Archipelago wolf includes the islands south of Frederick Sound and the narrow strip of land west of the Coast Mountains that extends from Dixon Entrance northward to Yakutat Bay (Hall 1981) (Fig. 3). Pedersen's (1982) morphological analysis of wolves in Alaska concluded that C. l. ligoni was a distinct population within Alaska and supported Goldman's subspecific classification. Nowak (1983) and Friis (1985) also provided morphological data indicating that Archipelago wolves represented a distinct population; however, both authors suggested that C. l. ligoni may be a remnant population of a larger subspecific group that once occupied the 48 contiguous United States. Recently, Nowak (1994) concluded a morphological survey of wolves in
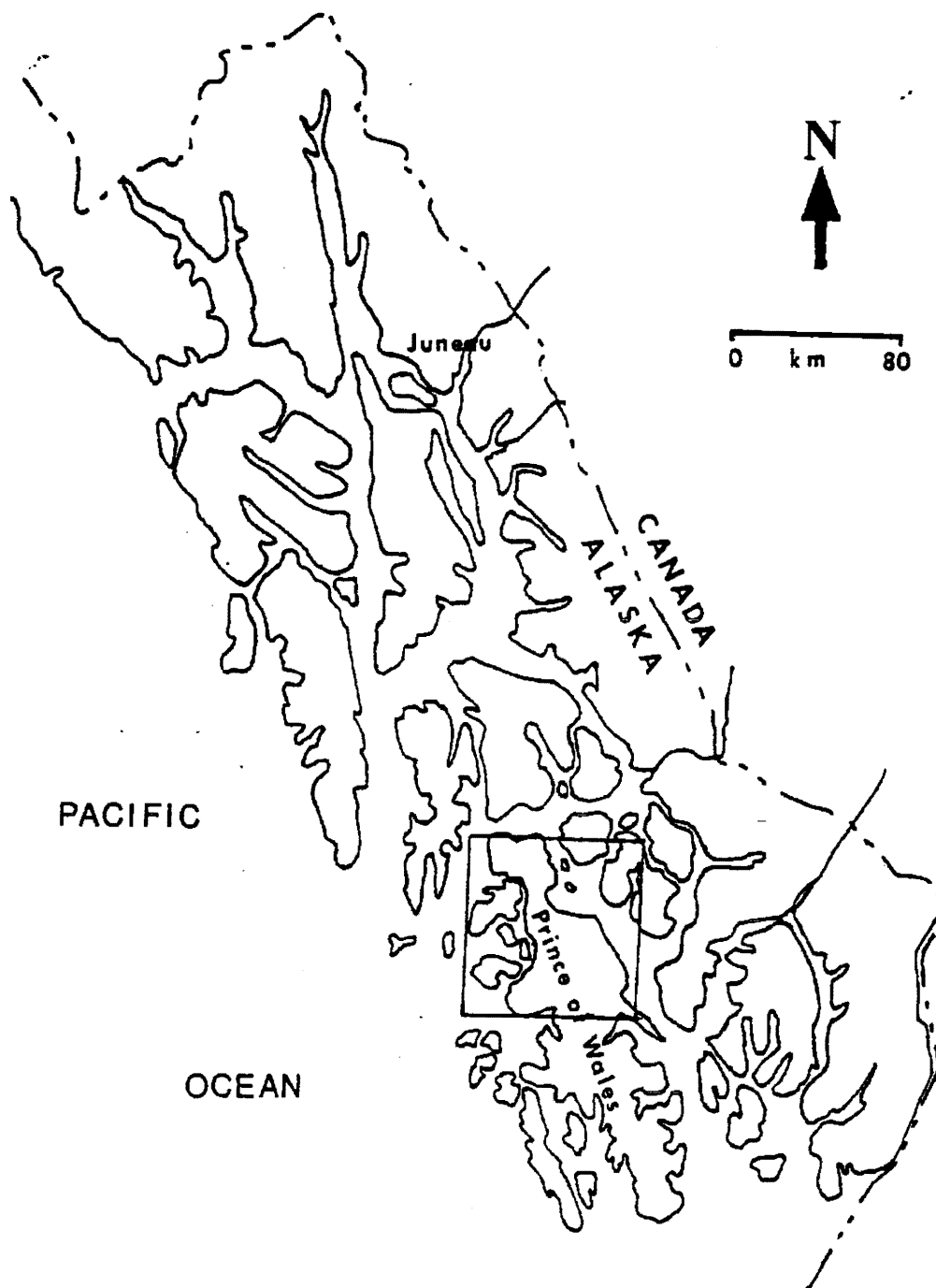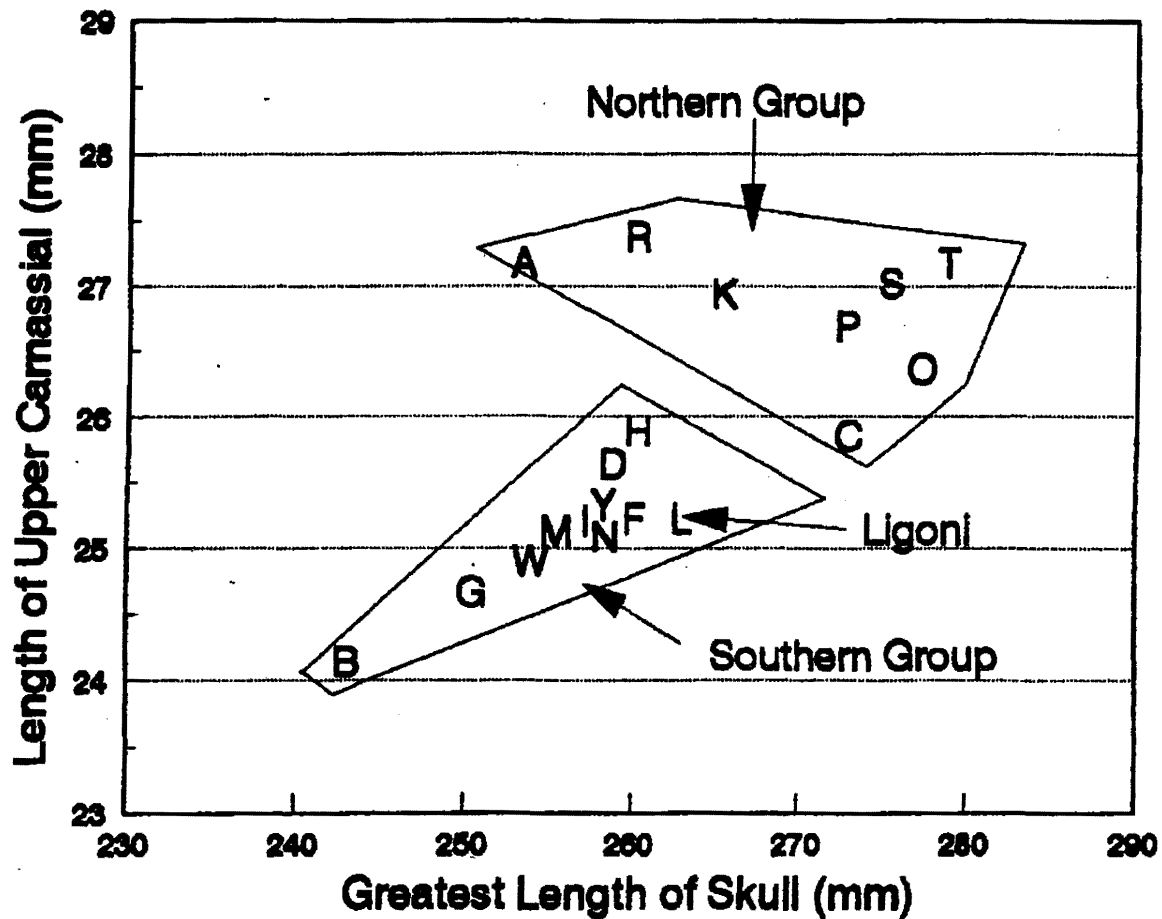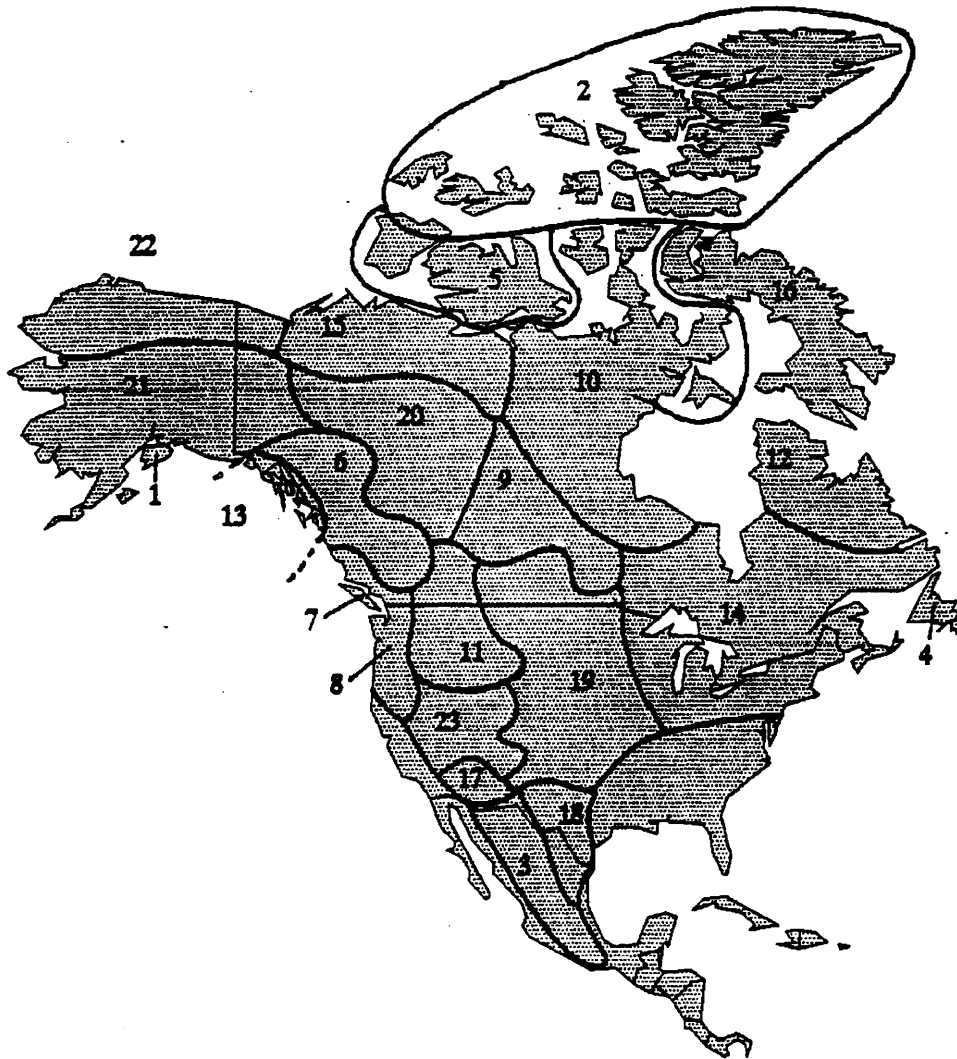
Figure 1. Alexander Archipelago in southeast Alaska. Box indicates location of study area to be used during the intensive phase of this research.

Figure 2. Bivariate analysis of measurements of the skulls of males of 19 subspecies of wolves, showing relationship of skull length to upper carnassial length. Adapted from Nowak (1983).

1. C. l. alces	7. C. l. crassodon	13. C. l. ligoni	19. C. l. nubilus
2. C. l. arctos	8. C. l. fuscus	14. C. l. lycaon	20. C. l. occidentalis
3. C. l. baileyi	9. C. l. griseoalbus	15. C. l. mackenzii	21. C. l. pambasileus
4. C. l. beothucus	10. C. l. hudsonicus	16. C. l. manniingi	22. C. l. tundrarum
5. C. l. bernardi	11. C. l. irremotus	17. C. l. mogollonensis	23. C. l. youngi
6. C. l. columbianus	12. C. l. labradorius	18. C. l. monstrabilis	

Figure 3. Locations of grey wolf (Canis lupus) subspecies in North America. Adapted from Hall (1981).

North America and suggested that C. l. ligoni may be a remnant population of C. l. nubilus, which once occupied central and southwestern Canada as well as the western contiguous United States (Fig. 4), and whose range has been reduced to central Canada, Minnesota, and perhaps southeastern Alaska (Fig. 5). Nowak questioned whether the Alexander Archipelago wolf deserves a unique subspecific status; however, regardless of its status, C. l. ligoni may be a unique genetic population whose closest relatives are in Minnesota, over 2,000 miles away.

Wolves probably gained access to the mainland strip and most of the islands in the southern portion of the Alexander Archipelago because sea level was lower during the first few thousand years of the current post-glacial period (Klein 1965). Fossil remains of Sitka black-tailed deer from Prince of Wales Island indicate that they were present at least 8,300 years ago (Baichtal pers. comm.). It is reasonable to assume that wolves arrived shortly thereafter, and may have colonized southeastern Alaska between 7,000 and 8,000 years before present. As sea level rose, land bridges disappeared and open water distances between islands increased, potentially isolating major island clusters such as Prince of Wales and the adjacent islands. Consequently, the wolf population in southeastern Alaska may be fragmented into several independent subpopulations between which migration is restricted.

The current wolf population estimate for southeastern Alaska is 900 to 1,000 individuals (Kirchhoff pers. comm.) and is based on data collected by Alaska Department of Fish and Game (ADF&G) personnel from field observations, trappers, and other sources of anecdotal information. Census and harvest data suggest that both wolf and deer populations peaked in the mid-1960s, declined during the 1970s, and began increasing again in the mid-1980s (ADF&G, unpublished data). Nonetheless, if the Archipelago wolf population is fragmented, it is unlikely that population trends would be consistent among subpopulations unless synchronized by factors such as weather that would affect prey populations regionwide. Furthermore, total population estimates would be largely irrelevant as a guide for management and would need to be replaced by estimates for each independent subpopulation.

Wolf population levels are generally dependent on prey abundance (Packard and Mech 1980, Keith 1983, Messier 1985, Fuller 1989). Therefore, the distribution, abundance, and stability of Archipelago wolf populations are probably a dynamic function of geography and deer populations. Deer are the wolves' principal prey, although spawning salmon (Oncorhynchus spp.) and beaver (Castor canadensis) appear to be seasonally important in their diets (Smith et al. 1987, Person 1993).
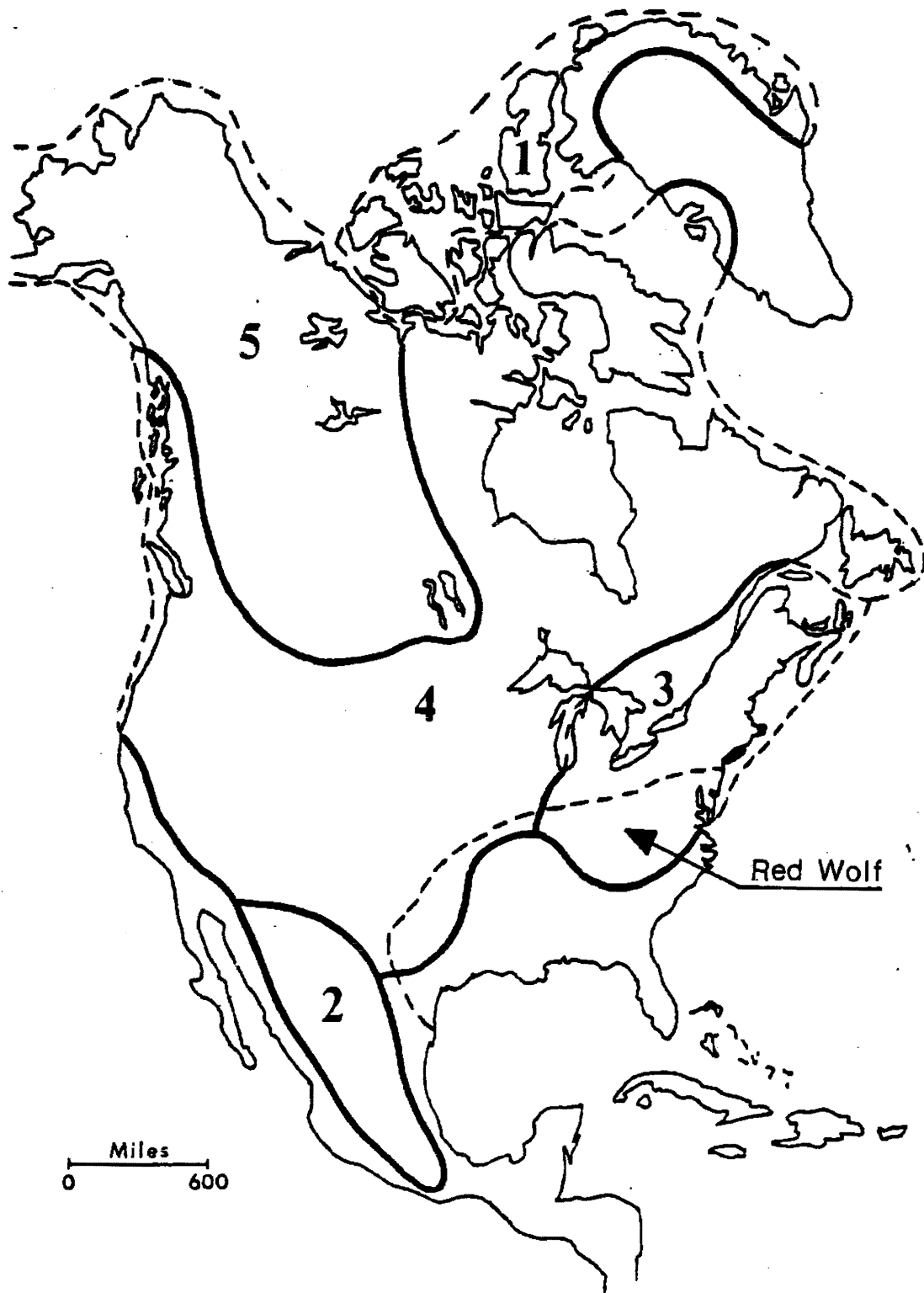
Figure 4. Revision of wolf taxonomy proposed by Nowak (in press). Current subspecies are lumped into 5 groups: 1) <u>Canis lupus arctos</u>, 2) <u>C. l. baileyi</u>, 3) <u>C. l. lycaon</u>, 4) <u>C. l. nubilus</u>, and 5) <u>C. l. occidentalis</u>.
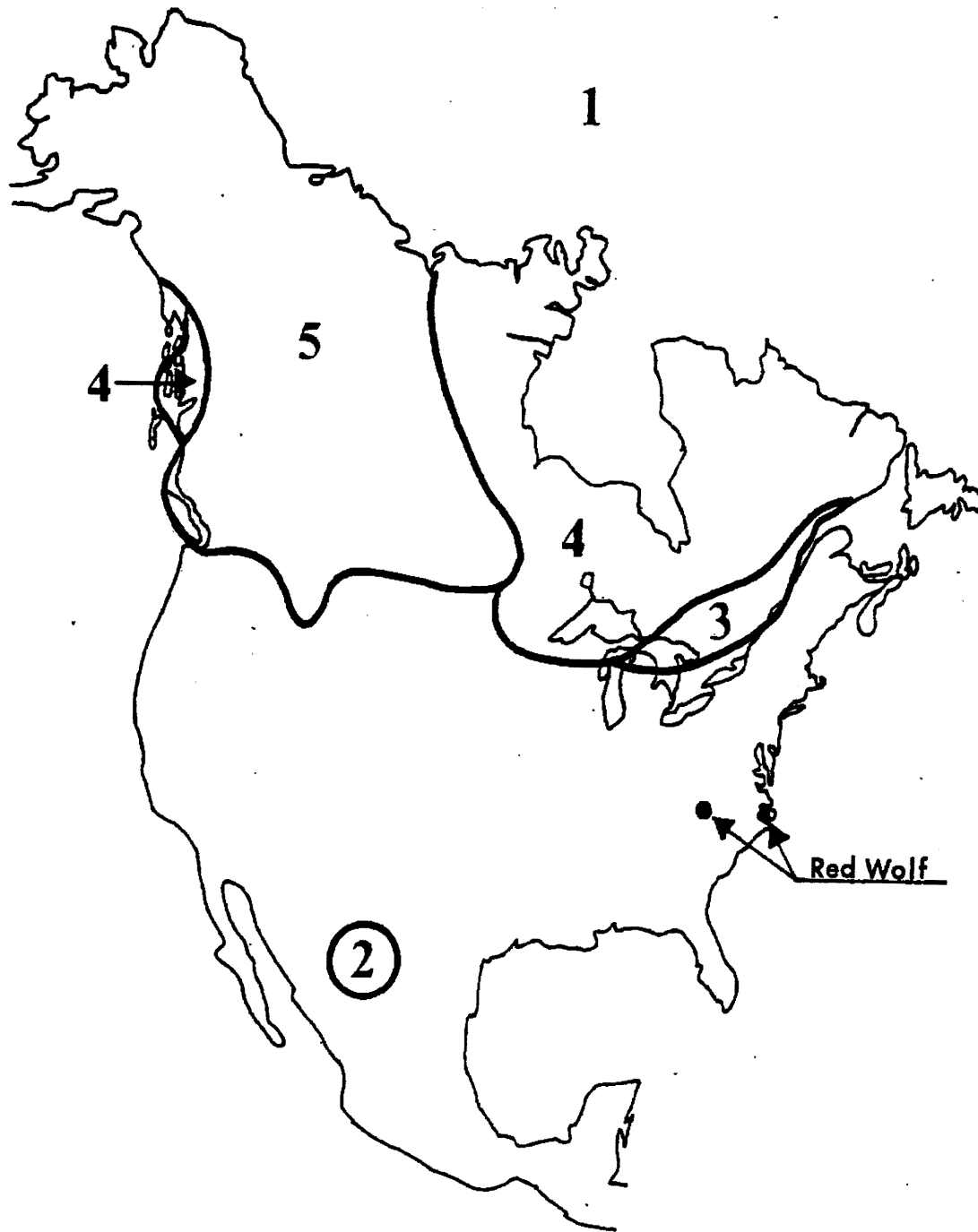
Figure 5. Current range of subspecies proposed by Nowak (in press).

Wolf population dynamics will probably be complicated by impending habitat changes (Van Ballenberghe and Hanley 1984). Approximately 80 to 90% of the range of the Archipelago wolf lies within the Tongass National Forest, where 800,000 hectares of commercially valuable forest are scheduled to be clearcut under the current forest management plan (USFS 1991). This represents 35-37% of the total commercially valuable timber on Tongass National Forest lands (USFS 1993). It is, however, a misleading statistic because several ecological provinces or major island groups are being harvested at a much higher rate. For example, under the current forest plan, over 60% of the commercially valuable timber will be cut on Prince of Wales Island (USFS 1993), including most of the low elevation, high-volume stands that are important deer wintering habitat. Forage available to deer is extremely limited in second-growth stands greater than 20 to 30 years old (Wallmo and Schoen 1980, Schoen and Kirchhoff 1985). Consequently, carrying capacity for deer is expected to decline as much as 60% from historical levels in some ecological provinces (USFS 1993) and deer numbers will decline (Wallmo and Schoen 1980, Hanley 1984, USFS 1991). It is therefore reasonable to speculate that timber harvesting will also play a major role in determining wolf distribution and abundance. In addition, if the wolf population functions as a collection of smaller, local subpopulations associated with the major island clusters and mainland sections, any subpopulation reduced as a consequence of habitat change may have a low probability of benefiting from a "rescue effect" by migrants from neighboring subpopulations.

OBJECTIVES AND RESULTS TO DATE

The Archipelago wolf presents a difficult challenge to wildlife managers: the conservation of a large predator in a highly fragmented environment that is undergoing rapid and long-term habitat change. The task is made more difficult because little is known about the basic ecology of the wolf in southeastern Alaska, although much is known about wolves elsewhere.

To predict future trends in Archipelago wolf populations, we need to know how wolves respond spatially, behaviorally, and numerically to changes in habitat composition. To address this question, we are conducting a two-part study that combines an extensive inventory of wolf distribution and abundance with an intensive investigation of the spatial organization, movements, habitat use, and feeding ecology of wolves.

Study Area

The Alexander Archipelago is located in southeastern Alaska between Yakutat Bay and Dixon Entrance. The study area comprises Prince of Wales and

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the adjacent islands. Island sizes range from over 5900 km² to less than 30 km², and distances between islands vary from 12 km to less than 1 km. Winters are generally mild with highly variable snowfall; snow accumulations are intermittent. Timber harvesting has occurred in the area since the early 1900s; to date, approximately 400,000 acres of old-growth forest have been cut and over 3000 miles of road have been built on Prince of Wales Island (USFS GIS database, 1993).

Dense coniferous rain forests of Western hemlock (Tsuga heterophylla), Sitka spruce (Picea sitchensis), yellow cedar (Chamaecyparis nootkatensis), and red cedar (Thuja plicata) cover large portions of the area. Understory vegetation varies depending on light, soils, and logging history (Alaback 1982). Vaccinium spp., Menziesia ferruginea, Cornus canadensis, Rubus pedatus, Coptis asplenifolia, and Oplopanax horridus are common species of forbs and shrubs found in the region. Generally, very little vegetation is found under second-growth forest greater than 20 to 30 years old. Muskeg bogs cover large portions of some islands. Wolf, deer, and beaver populations appear to be at high levels throughout the study area (Larsen pers comm.). In addition, the region supports black bears (Ursus americanus), river otters (Lutra canadensis), mink (Mustela vison), and numerous small mammals.

Objective 1: Distribution and Abundance of Wolves

Historical records should enable us to identify islands and other land areas that have maintained persistent wolf populations and will be used to gain a historical perspective about wolves in southeastern Alaska. In addition, an extensive survey of the current distribution and abundance of wolves in a portion of the Ketchikan area that includes Prince of Wales and adjacent islands is being done using aerial observations, track surveys, harvest records, and infrared-triggered cameras.

Results to Date:

We have contacted wolf trappers, hunters, fishermen, native Alaskans, biologists, and foresters who have supplied valuable information about the presence and absence of wolves throughout the region. We also have compiled historical bounty, trapping, and sealing records into a spreadsheet database. These data show that wolves are distributed throughout Game Management Unit (GMU) 2, which includes Prince of Wales and the adjacent islands (Table 1). Data from the last 40 years suggest, however, that only Prince of Wales, Kosciusko, and possibly Dall Islands are sufficiently large to maintain persistent wolf

Table 1. Distribution of wolves on major islands in GMU 2[*]. Temporary population status is assigned if evidence exists that the island was unoccupied by wolves at some time in the last 40 years or if wolves currently occupying the island leave it periodically and return. Permanent status indicates that an island has been continuously occupied over at least the last 40 years.

Island	Status of Wolf Pop.	No. of Packs
Prince of Wales	Permanent population	22-24
Kosciusko	Permanent population	1-2
Dall	Permanent population	?
Heceta	Temporary population	1
Suemez	Temporary population	?
Sukkwan	No data	?
Long	Temporary population	Occasional wolves from Dall
Baker	Temporary population	1
Noyes	Temporary population	Probably same pack as Baker
Lulu	Temporary population	Probably same pack as Baker
San Fernando	Temporary population	?
Tuxekan	Temporary population	Occasional wolves from POW
Warren	Temporary population	Occasional wolves from Kosciusko
Marble	Temporary population	Occasional wolves from POW or Kosciusko
Orr	Temporary population	Occasional wolves from POW or Kosciusko
Thorne	Temporary population	?
San Juan Baptiste	Temporary population	Occasional wolves from POW

* Data are based on sealing and bounty records, discussions with local hunters and trappers, information provided by USDA Forest Service and ADF&G personnel, aerial and ground surveys, and radio-telemetry relocations. Although some islands, such as Baker, Lulu, and Noyes, are not large enough individually to support a wolf pack, they may do so collectively.

populations completely within their boundaries. The other islands in GMU 2 appear to be occupied intermittently or are currently used as a portion of a pack's home range that includes several islands. The persistence of wolves on Kosciusko Island may be a function of its close proximity to Prince of Wales Island, which would facilitate dispersal and immigration. Indeed, considering the narrow width of Dry Pass at low tide, Kosciusko Island could be considered a peninsula of Prince of Wales Island. Simulations of a wolf-deer population model (Person 1993) indicate that a land area of 2000-3000 km^2 may be necessary to ensure a persistent wolf population given an average deer population carrying capacity of 7-10 deer/km^2. These results would suggest that Prince of Wales Island likely supports the only permanent wolf population in GMU 2 in the absence of immigration from some other source.

We estimate the wolf population on Prince of Wales Island (including Kosciusko Island, considered as a peninsula of Prince of Wales Island) to be between 300-330 wolves (mean = 317, 95% C. I. = ± 12). This value represents the mean of 500 simulated populations based on estimates of pack home ranges, home-range overlap, pack sizes, and number of dispersers in the population derived from observations of our radio-collared animals (Fig. 6). We did not include wolves occupying Dall, Heceta, or the outside islands because of a lack of data with respect to home ranges, home-range fidelity, pack sizes, and movements. Therefore, our estimate does not include all of GMU 2.

Each simulated population was calculated by multiplying home range by the fraction of home range that is exclusive to each pack. The product was then divided into the combined land area for Prince of Wales and Kosciusko Islands to estimate the maximum number of resident packs. We assumed that all land area is occupied, although this method probably overestimates the true number of packs. The number of packs was then multiplied by pack size to estimate the resident wolf population. Finally, the resident population was divided by the fraction of the total population that they represent, to account for dispersing wolves that are not residents. Each input value was a random, normal variate distributed with a mean and variance calculated from empirical data gathered during this study. The estimate represents the maximum fall 1994 population prior to the beginning of the trapping season.

Wolf population density on Prince of Wales is estimated to be 49 wolves per 1000 km², which is comparable to densities reported from Vancouver Island (Hebert et al. 1982), and is generally higher than reported for wolves in other portions of North America where deer are the principal prey (Fuller 1989). Fuller (1989) reported fall population densities as high as 59 wolves per 1,000 km² in north-central Minnesota; however, wolf density that exceeded 40 per 1,000 km² in a given year always resulted in a decline the following year.

Wolves on Prince of Wales and Kosciusko Islands probably account for 33 to 37% of the total wolf population in southeastern Alaska. This is consistent with the distribution of the wolf harvest in southeastern Alaska, in which 47% of the wolves killed are from GMU 2 (Kirchhoff pers. comm.). Considering the wide distribution of the human population and accessibility of most of the area by boat and an extensive road system, it is reasonable to assume a disproportionately high harvest with respect to actual wolf population density in GMU 2.
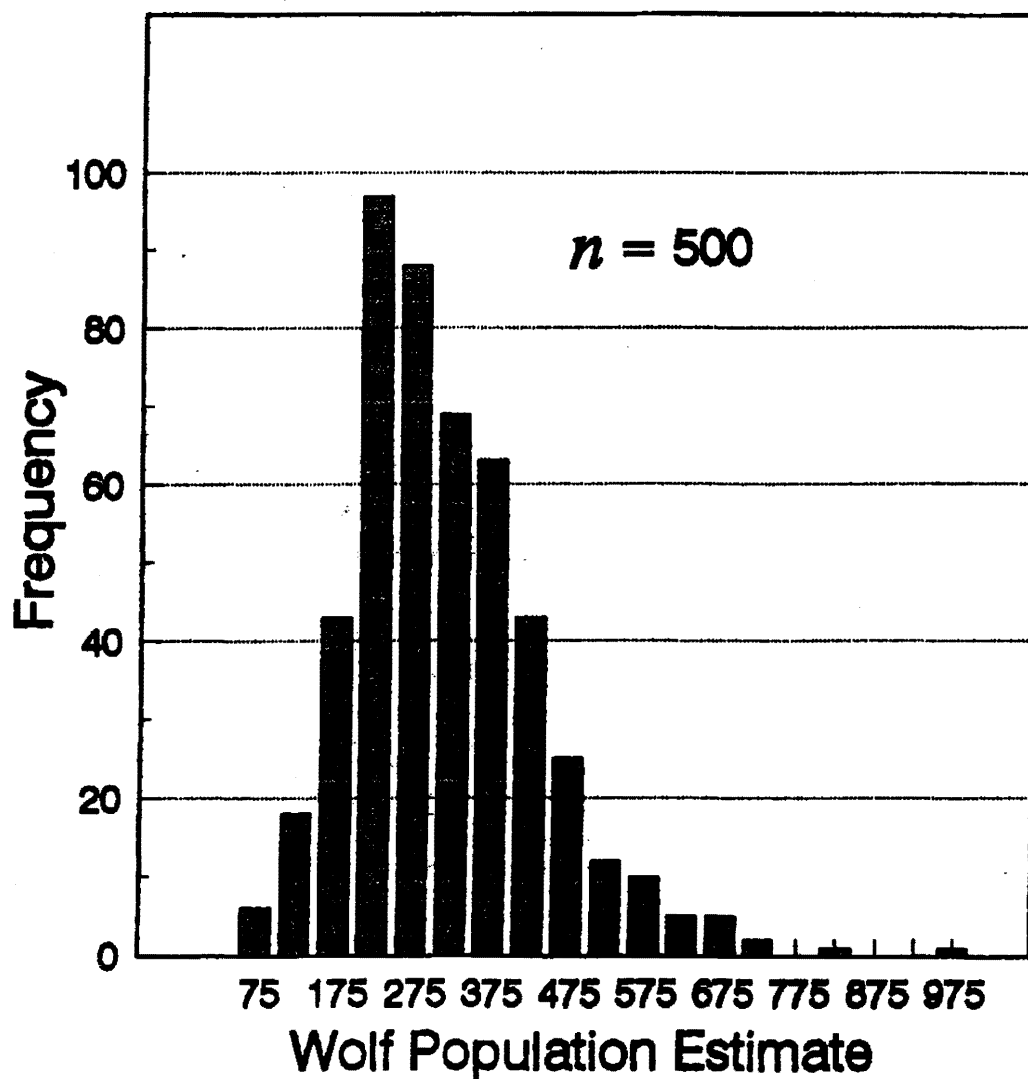
Figure 6. Frequency histogram showing population simulations based on home-range size, pack size, and percent dispersers in the population. Estimates are for fall wolf population on Prince of Wales and Kosciusko Islands during 1994.

Our original plan was to study radio-collared wolves with respect to 3 broad landscape types defined by the level of timber harvesting characteristic of the forested portion of the area:

Type 1--extensively logged, dominated by second growth >20 years old (western Kosciusko Island, Harris River);

Type 2--extensively logged, with an interspersion of older and younger (<20 years) second-growth stands with uncut old-growth stands (Staney Creek area, Thorne Bay, Ratz Harbor-Big Lake area); and

Type 3--unlogged or lightly harvested area encompassing a mixture of old-growth timber volume classes (Honker Divide, Nossuk Bay-Salt Lake Bay area, eastern Kosciusko Island).

In essence, these types represent landscapes of the future, the present, and the past. During this study, it was apparent that no wolf pack home ranges were confined to any one distinct landscape type. All packs studied overlapped logged areas extensively and it became clear that our original landscape divisions were not biologically meaningful. Consequently, future analysis will test hypotheses concerning home range versus habitat composition rather than defined landscape types.

Results to Date:

Capture and Immobilization of Study Animals.--Thirty-one wolves were captured between February 1993 and November 1994. Twenty-four of these animals, representing 8-10 different packs, were radio-collared and released. Of the 7 wolves not instrumented, one was euthanized because of trap-related injuries, one was killed in the trap by other wolves, one escaped from an experimental padded-jaw trap, two broke the traps and escaped, one was stolen, and one was shot in the trap before we could process it. The first 2 wolves captured sustained severe injuries from the traps. Consequently, we installed cable clamps on the inside of the trap jaws, which increased the jaw offset (gap that remains between the jaws when they are shut) from 0.8 cm to 1.8 cm. In addition, we shortened the drag chains from 12 to 6 feet. Since these changes were made, no wolves have suffered serious injuries during capture.

Home-Range Analysis.--The 24 radio-collared wolves included 5 adult females, 6 adult males, 6 yearling females, 1 yearling male, 2 juvenile females, and 4 juvenile males (Table 2). The study animals represent 7-9 packs occupying Prince of Wales Island and one pack occupying Kosciusko Island. At the time

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Table 2. Age, sex, weight, and pack membership for radio-collared wolves captured between February 1993 and December 1994. Current pack-size estimates are based on evidence from aerial observations and ground surveys of tracks and scats.

Wolf ID	Age	Sex	Weight (kg)

Ratz Harbor Pack   (7 wolves in 1994)

AF78	Adult	Female	36.4 kg
-- Dispersed in January 1994			
YM76	Yearling	Male	29.5 kg
AM80	Adult	Male	34.1 kg

Thorne River Pack? (pack size unknown, at least 3 wolves in 1993) This pack may have dissolved or been absorbed by the Honker Divide pack in the fall of 1993.

YF80	Yearling	Female	27.3 kg

Honker Divide Pack   (12 wolves in 1994)

YF74	Yearling	Female	27.3 kg
JM61	Juvenile	Male	25.0 kg
AM63	Adult	Male	38.6 kg
-- Dispersed March 1994			
JF65	Juvenile	Female	27.2 kg

Twin Spurs Pack   (8 wolves in 1994, possibly 11-12 in 1993)

JM79	Juvenile	Male	25.0 kg
YF60	Yearling	Female	27.3 kg
AM64	Adult	Male	31.8 kg
JF65a	Juvenile	Female	25.5 kg
AF82	Adult	Female	31.8 kg
JM64	Juvenile	Male	19.1 kg

The following wolves may have been members of this pack in 1993:

AF73	Adult	Female	34.1 kg
YF82	Yearling	Female	29.5 kg

Tuxekan-Naukati Pack? (7 wolves in 1993) This group may not be a distinct pack but may be members of the Twin Spurs, Nossuk Bay, or Sarkar packs. To date we have not obtained sufficient data to clarify this.

AM62	Adult	Male	34.1 kg
-- Dispersed in February 1994			

Table 2. Continued.

Wolf ID.	Age	Sex	Weight
Kosciusko Pack (9 wolves in 1993, 4? in 1994)			
YF77	Yearling	Female	29.5 kg
YF81	Yearling	Female	34.1 kg
-- Dispersed in January 1994			
AM75	Adult	Male	34.1 kg
-- Dispersed in May 1994			
Karta Pack (Pack size unknown)			
AF57	Adult	Female	36.4 kg
Sarkar Pack (Pack size unknown)			
JM66	Juvenile	Male	32.7 kg
-- Dispersed in March 1994			
Kasaan Pack (2 wolves in 1994)			
AF78			
-- Immigrant from Ratz Harbor pack in January 1994			
Nossuk Bay Pack (7 wolves in 1994)			
AF62	Adult	Female	30.4 kg
Transients or Dispersers?			
AM59	Adult	Male	35.9 kg

of capture, one wolf (AM59) was a disperser, which we define as an animal exhibiting large movements without an identifiable home range. Subsequent to capture, 6 others wolves dispersed (YF81, JM66, AF78, AM75, AM63 and AM62), 3 of which eventually established home ranges after dispersing. Five other wolves (AM64, YF82, YF74, JM61, and AF73) displayed extraterritorial movements. These animals established home ranges (or were in the process of doing so prior to their deaths or loss of contact) that encompassed the natal home range, but were larger. These extraterritorial home ranges overlapped neighboring pack home ranges extensively.

The other 12 wolves remained within the home ranges they occupied at the time of capture until 1 December 1994 (the period covered by this report) or until they died. They were observed interacting with other wolves and were considered part of a resident pack. One adult female wolf (AF82) captured in late summer showed evidence of having raised pups and was probably the alpha female of that pack.

To date, a total of 1,241 radio relocations have been recorded both from the ground and from aircraft. Approximately 20% of these observations were at night. Ground-based observations were usually recorded by a single observer, although simultaneous azimuths by two observers were taken on many occasions. Time lags between azimuths generally ranged between 3-15 minutes. Accuracy and precision of ground-based telemetry were estimated by blind-testing observers with transmitters in fixed locations, then periodically retesting observers with randomly located transmitters. Testing simulated good-quality signals representing stationary animals and poorer-quality signals representing moving animals. Precision was estimated at ± 4.5° for good-quality signals and ± 9° for poorer-quality signals. Signal modulation was used to determine activity. Radiolocations with error polygons $\geq$ 50 hectares were deleted from the data. This eliminated between 3 and 18% of the ground-based telemetry data, depending on the study animal. After editing, the average error polygon was 8 hectares (95% C. I. = ± 1). The accuracy of aerial observations has not been determined quantitatively, but the error associated with aerial relocations is undoubtedly much less than that associated with ground-based telemetry.

For this report, radiolocations were tested for autocorrelation by deriving autocorrelation functions for x coordinates, y coordinates, and cross correlation functions for x versus y coordinates (Person and Hirth 1991). In addition, Spearman rank correlations were calculated for distances moved versus time-lag between observations (Person and Hirth 1991). Data showing no significant correlations in three of the four tests were judged to be independent (in this case, lack of autocorrelation is used to indicate statistical independence).

Mohr's minimum convex polygon (MCP) and 95% adaptive kernel (ADK) (Worton 1989, Kie 1994) home ranges were estimated for 9 resident wolves and 3 wolves exhibiting extraterritorial movements (Table 3), each with more than 30 relocations. Home ranges were also estimated for 6 packs (Table 3, Fig. 7). Seventy-five percent adaptive kernel home ranges were used to define core areas. The average 95% ADK home range for resident wolves was 274 km² (± 94) and the average MCP home range was 226 km² (± 67). These home-range estimates are considerably larger than those previously reported (Person 1993) because they reflect the inclusion of winter data. Core areas averaged 98 km² (± 60), which suggests that on average, wolves spend 75% of their time within only 30 to 40% of their home ranges. Pack home ranges averaged 296 km² (± 182) for 95% ADK home ranges and 264 km² (± 127) for MCP home ranges. Pack sizes ranged from 2 to 12 wolves with an average of 8 to 9 animals. Pack home range was not correlated with pack size ($r = 0.06$, $P = 0.9$) even after the large home range for the Kosciusko pack was deleted from the analysis.

Table 3. Mohr's convex polygon and adaptive kernel home ranges for 12
wolves and 6 packs on Prince of Wales Island between March 1993 and December
1994.

	HOME RANGES (in km^2)			
	Mohr's Convex Polygon	95% Adaptive Kernel	75% Adaptive Kernel	n
Residents				
AF78*	298	325	148	54
AF78**	167	187	52	31
AF82	118	185	42	32
AM80	212	371	116	45
YF74	335	330	101	83
YF77	353	513	278	46
YF80	159	141	43	63
YM76	250	274	61	128
JM79	138	143	40	115
MEAN (95% C.I.)	226 (± 67)	274 (± 94)	98 (± 60)	

* Home range prior to dispersing
** Home range after dispersing to different location

	Mohr's Convex Polygon	95% Adaptive Kernel	75% Adaptive Kernel	n
Pack Home Ranges				
Honker	270	340	90	101
Kasaan	167	187	52	31
Kosciusko	464	586	200	96
Ratz Harbor	343	376	85	224
Thorne River	159	141	43	63
Twin Spurs	181	148	50	154
MEAN (95% C.I.)	264 (± 127)	296 (± 182)	87 (± 62)	

	Mohr's Convex Polygon	95% Adaptive Kernel	75% Adaptive Kernel	n
Extraterritorial Home Ranges				
AF73	310	---	---	52
AM64	747	---	---	59
YF82	351	---	---	73

A. Kosciusko Island Pack
B. Twin Spurs Pack
C. Honker Divide Pack
D. Ratz Harbor Pack
E. Kasaan Pack
F. Thorne River Pack
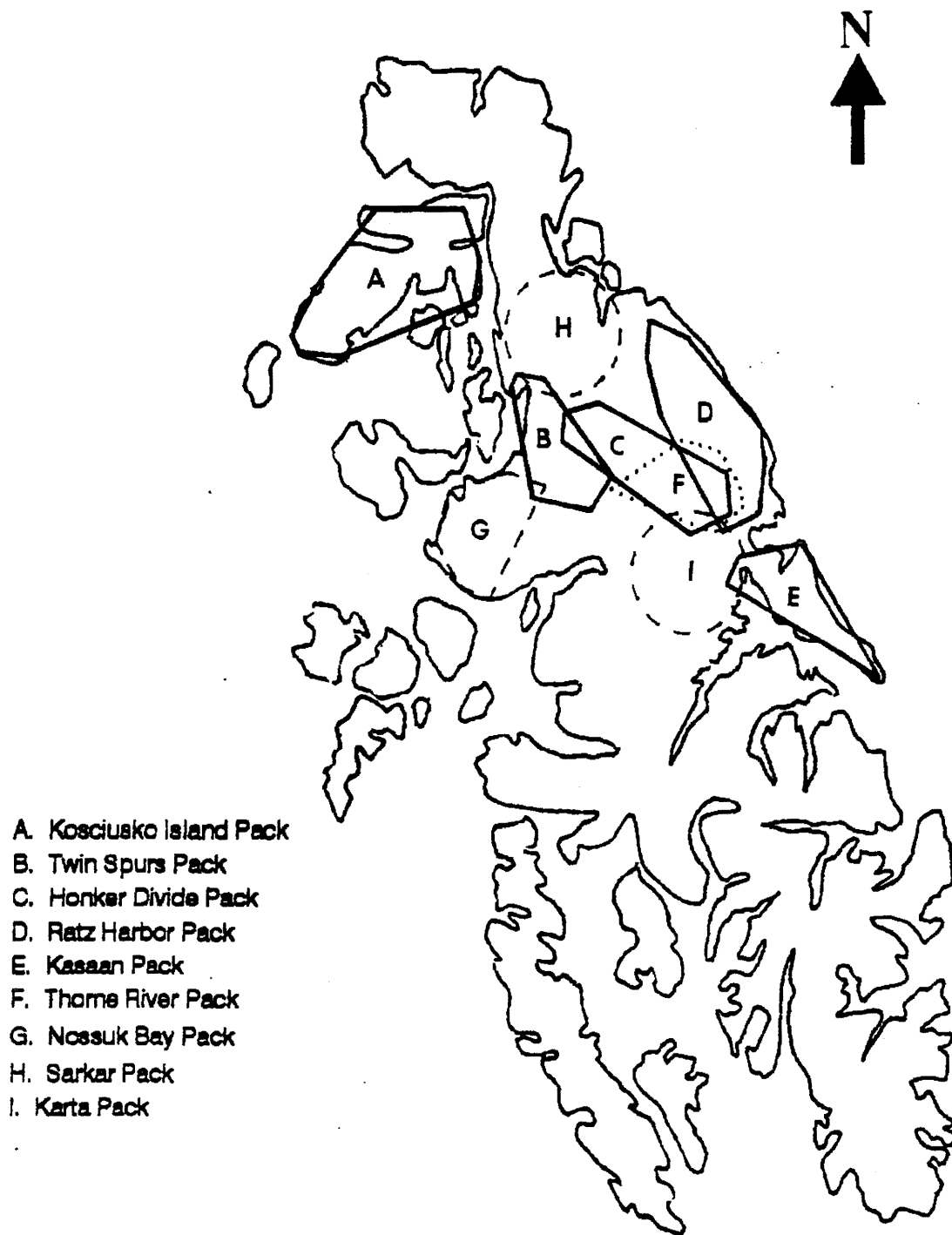G. Nossuk Bay Pack
H. Sarkar Pack
I. Karta Pack

Figure 7. Home ranges and locations for 9 wolf packs on Prince of
Wales and Kosciusko Islands. Solid lines show minimum
convex polygon home ranges for packs with greater than
30 radiolocations. Dotted line shows home range of
Thorne River pack in 1993. Dashed lines show approximate
home range boundaries for packs with less than 30 radio-
locations.

Pack home ranges for wolves on Prince of Wales Island appear to be large compared to home ranges of wolf packs reported in other studies where the primary prey is deer (Table 4). Fuller (1989) reported a strong negative correlation between pack home ranges and deer density for wolves studied in Minnesota and Canada. We repeated Fuller's (1989) weighted regression analysis (weights = n) and compared home ranges estimated for wolf packs on Prince of Wales Island to the model (Fig. 8). The results suggest that pack home ranges reported in this study are larger than would be expected based on deer density. Wolves use second-growth habitat very infrequently, however (see subsequent sections of this report for results of habitat-use analysis), and if the area of second growth is subtracted, the pack home ranges estimated for this study are more in line with what would be predicted by deer density (Fig. 8).

With respect to home range, the Kosciusko Island pack presents an interesting case study. In 1993, we estimated pack size to be 9 wolves based on direct observations. During summer and fall 1993, this group exhibited one of the smallest home ranges recorded for a pack that size (MCP = 28.9 km^2, Person 1993). They spent most of July, August, and September concentrating their activity in the southeastern lobe of the island while feeding on spawning salmon. During the winter of 1993-94, the pack home range expanded dramatically and activity shifted to the central and western portions of the island. Female wolf YF81 dispersed in January 1994 and adult male AM75 dispersed in May 1994. Both wolves eventually were found in the very southern portions of GMU 2.

In spring and summer 1994, female wolf YF77 (last remaining radio-collared wolf on Kosciusko Island) was observed on 3 occasions with 3 other wolves. During summer, field personnel working on the ground reported the absence of fresh wolf activity unless YF77 was located in the area. These data lead to the conclusion that this pack was reduced in size from 9 in 1993 to 4 in 1994. Furthermore, the pack occupies most of Kosciusko Island and has the largest home range reported in this study, suggesting that wolf density on the island has declined. Other wolves have been observed on the northeastern portion of the island, but we believe these animals originate from Prince of Wales Island and occasionally cross over to Kosciusko near Dry Pass. In 1993, the Kosciusko pack produced a litter of pups while occupying the southeastern lobe of the island. No denning activity was observed in 1994 and pack size appears to have remained constant into the fall, suggesting a lack of successful reproduction.

Table 4. Mean convex polygon home ranges (in km²) vs deer densities for wolf populations that prey primarily on deer.

Location	HR	N	Deer/km²	Reference
NE Minnesota	110	5	5.1	Van Ballenberghe et al. 1975
N-Central Minnesota	116	33	6.2	Fuller 1989
E-Central Ontario	175	4	7.0	Pimlott et al. 1969
N-Central Minnesota	192	3	6.0	Berg and Kuehn 1980
S Quebec	199	21	3.0	Potvin 1988
E-Central Ontario	224	1	3.1	Kolenosky 1972
NE Minnesota	243	11	2.1	Mech 1973
Prince of Wales Is.	264	6	5.6*	This study

* Sitka black-tailed deer are approximately 20-30% smaller than white-tailed deer; therefore, estimated deer density on Prince of Wales Island was multiplied by 0.74 to adjust density to a value comparable to these other studies.

Activity Patterns.--Radio-collared wolves are most active at night, which we define as the time period 1/2 hour after sunset to 1/2 hour before sunrise. For resident wolves, 61.1% of the radiolocations during nighttime indicated movement, compared to 40% in daytime ($P < 0.0001$, n = 515). Dispersing animals or those exhibiting extraterritorial movements showed the same pattern, with 54.7% of the radiolocations indicating movement at night versus 39.6% during daytime ($P < 0.001$, n = 234). Overall, residents were active 45.8% percent of the time, and dispersers or extraterritorial wolves were active 44.4% of the time. Comparable activity data are lacking for wolves in other parts of North America; however, considerable information is available for coyotes (Canis latrans). Camenzind (1978) and Andelt (1985) studied coyotes in areas remote from human disturbances and reported that they were most active during daytime. In contrast, Person (1988) reported primarily nocturnal activity for coyotes occupying areas subject to widespread human access.

Dispersal and Extraterritorial Behavior.--In addition to the 2 wolves from Kosciusko Island, 5 others showed dispersal behavior. The annual (1 June 1993 - 31 May 1994) dispersal rate was 39% (95% C.I. = ± 23%, n = 18). The average monthly dispersal rate was 5% (95% C.I. = 0% - 17%), with peaks occurring in January and March. Five of the 7 dispersers were adults, one was a yearling, and one was a juvenile. Minimum dispersal distances from the point of capture ranged between 13-181 km (Fig. 9).
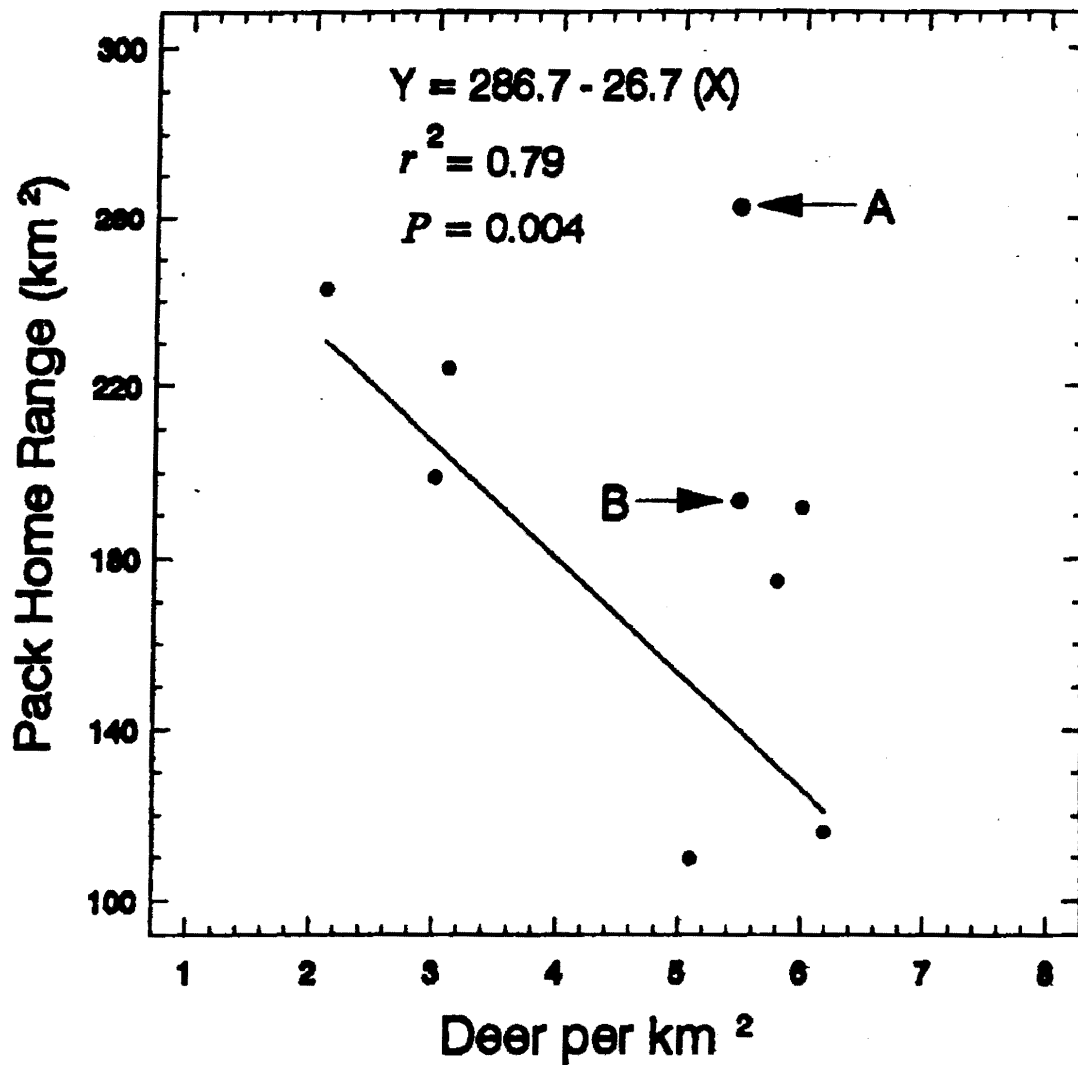
Pack Home Range (km²)

$Y = 286.7 - 26.7\ (X)$

$r^2 = 0.79$

$P = 0.004$

A

B →

Deer per km²

Figure 8. Weighted regression pack home range versus deer density for 7 studies throughout North America (adapted from Fuller 1989). Point A shows results from Prince of Wales Island for comparison. Point B shows the same data with area in second growth removed from home range.
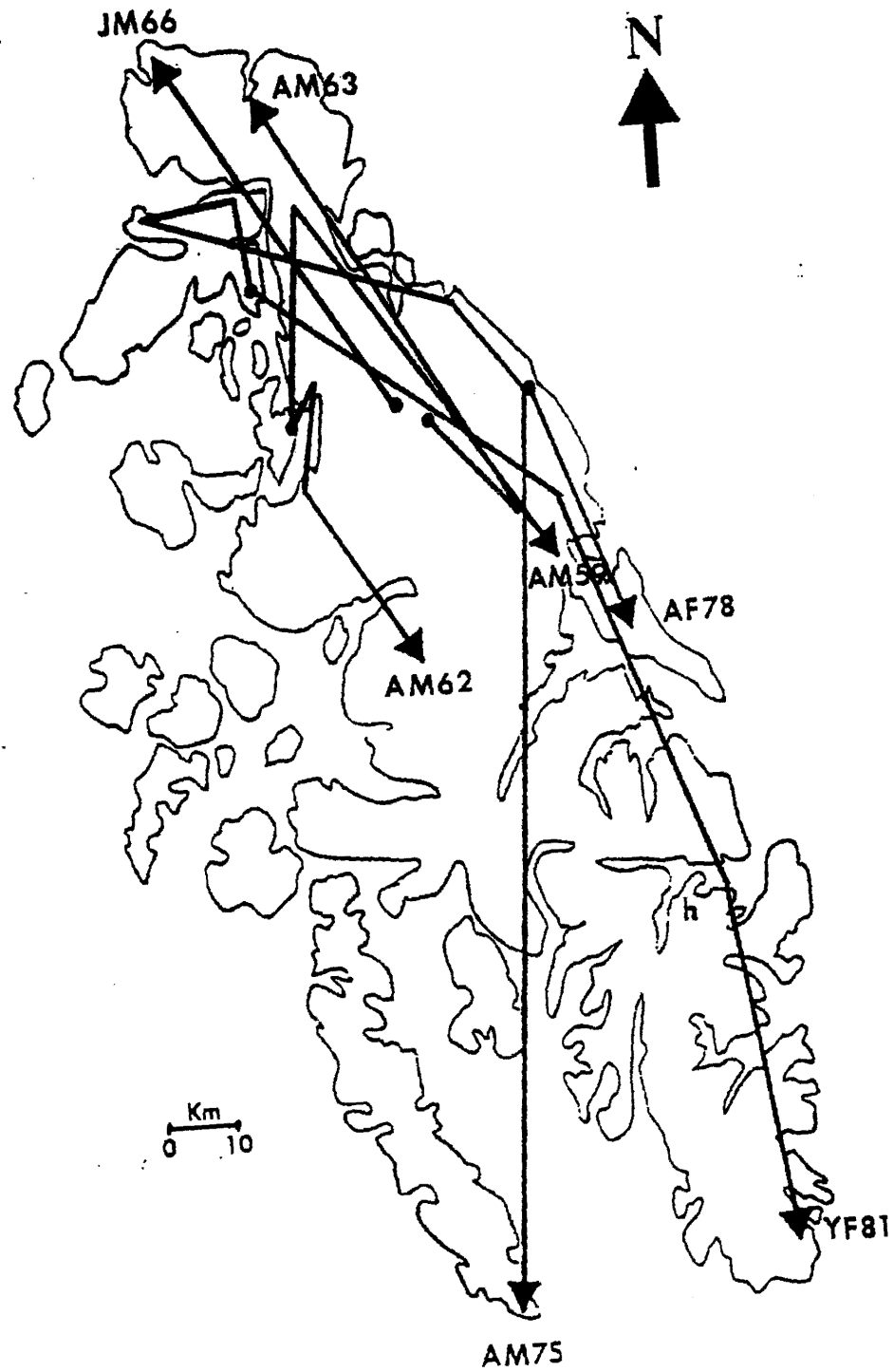
Figure 9. Minimum dispersal distances for wolves on Prince of Wales and Kosciusko Islands.

One adult male (AM59) was probably in the act of dispersing when captured. After capture on Tuxekan Island, he crossed over to Prince of Wales Island and was located near Sarheen Cove. Subsequently, he traveled to Neck Lake, then south past Luck Lake, and finally he disappeared near Thorne Bay. It is not known if he was killed or if his collar failed. Aerial searches were conducted over Etolin Island, the Cleveland Peninsula, and the mainland in order to eliminate the possibility that he migrated across Clarence Strait.

The longest dispersals were by 2 wolves from Kosciusko Island that eventually settled in the southern portion of GMU 2. One (YF81) took up residence near Mallard Bay on Prince of Wales Island, and the other (AM75) remained near Cape Muzon on Dall Island. AM75 has been observed 3 times and appears to be alone. However, YF81 was observed with a pack of 12 wolves near Cholmondeley Sound and may have failed in an attempt to join them.

Adult female AF78 was a member of the Ratz Harbor Pack until January 1994 when she dispersed southward towards Thorne Bay. She eventually settled on the Kasaan Peninsula where she has been observed on numerous occasions with one other wolf. A very old male (AM63) from the Honker Divide pack dispersed north to Red Bay and wandered between Red Bay and El Capitan before being shot in August 1994. The other 2 animals (AM62 and JM66) were shot or trapped while still dispersing.

The dispersal rates observed in this study are higher than those reported by Fuller (1989) in Minnesota or Peterson (1984) in south-central Alaska. The percentage of dispersing adults (45%) is high compared with rates observed in Quebec (Messier 1985) or Minnesota (Fuller 1989). The tendency for adults to disperse may be an indication of a reduction in wolf density in portions of the study area due to intensive trapping pressure. In addition, wolf harvests may disrupt the social hierarchy within a pack and induce dispersal. In the case of the Kosciusko pack, low prey density may be the principal cause.

The predominant direction of dispersal appears to be from north to south (5 of 7 dispersers traveled southward). None of the dispersers attempted to cross Clarence Strait, although 4 wolves did travel for a time along the eastern coastline of Prince of Wales Island. One wolf (AF78) was located on the tip of the Kasaan Peninsula and may have swum to Grindall Island before returning to the Kasaan. Their behavior was similar to that observed for dispersing coyotes in Vermont when faced with a large geographic barrier such as Lake Champlain (Person 1988). Conversely, all of the islands within 3-4 km of Prince of Wales or adjacent "stepping-stone" islands are accessible to wolves at least at slack tides. Our distribution and dispersal

data suggest that wolves in GMU 2 are a single, interbreeding population for which migration to the mainland is unlikely.

Five wolves exhibited extraterritorial movements (Fig. 10). Three of them, adult female AF73, yearling female YF82, and adult male AM64 were believed to originate in the Twin Spurs pack. Each animal maintained a large home range that overlapped at least a portion of their suspected natal home range. Female AF73 was alone, but YF82 and adult male AM64 appeared to be accompanied by at least one other wolf on several occasions. AM64 was directly observed to interact with members of the Twin Spurs pack both during the denning period (15 April - 1 August) and later in the fall. He currently maintains a home range that is estimated at 747 km², overlapping portions of the Twin Spurs, Honker Divide, Nossuk Bay, Sarkar, and Ratz Harbor packs. Fuller (1989) suggests that extraterritorial forays may precede dispersal, but AF73, YF82, and AM64 did not disperse during the period they were monitored (≥ 6 months). Yearling female YF74 and juvenile male JM61 of the Honker Divide pack made forays outside the natal home range while accompanied by at least one other wolf. Unfortunately, YF74 was shot, and pack members apparently chewed the collar off the neck of JM61 before we were able to establish the extent and duration of their extraterritorial movements.

Denning Ecology.--Wolves on Prince of Wales appear to den between 15 April and 1 August (n = 4). During denning, home ranges of resident wolves contracted to approximately 25 to 55% of their winter (nondenning season) size (Fig. 11). Activity is probably concentrated at the den site from mid-April to the first or second week in June. Pups have been observed making short forays from the den as early as the fourth week in May. By late July, den usage is minimal and by August the dens are abandoned until the next season. The same den sites may be used in consecutive years, but we can only verify den-site fidelity for one pack.

We examined 7 den sites between October 1992 and November 1994. All dens were located in old-growth stands within 100 m of fresh water. Most dens (6) were in holes located in the root wads of trees in excess of 1 m dbh; however, one den was located under a hollow log. Dens generally had several entrances ranging from 0.45 to 0.80 m in width, with the main entrances facing east or southeast.

The largest den examined had several tunnels 2-4 m in length connecting different root wads and was used by the Ratz Harbor pack for a minimum of 3 consecutive years prior to 1994. The pack did not return to the den in 1994, but chose a poorer site 12 km further north. We do not know why these wolves abandoned their original denning area; however, they left the area shortly after road-building activity near the den began in July 1993.
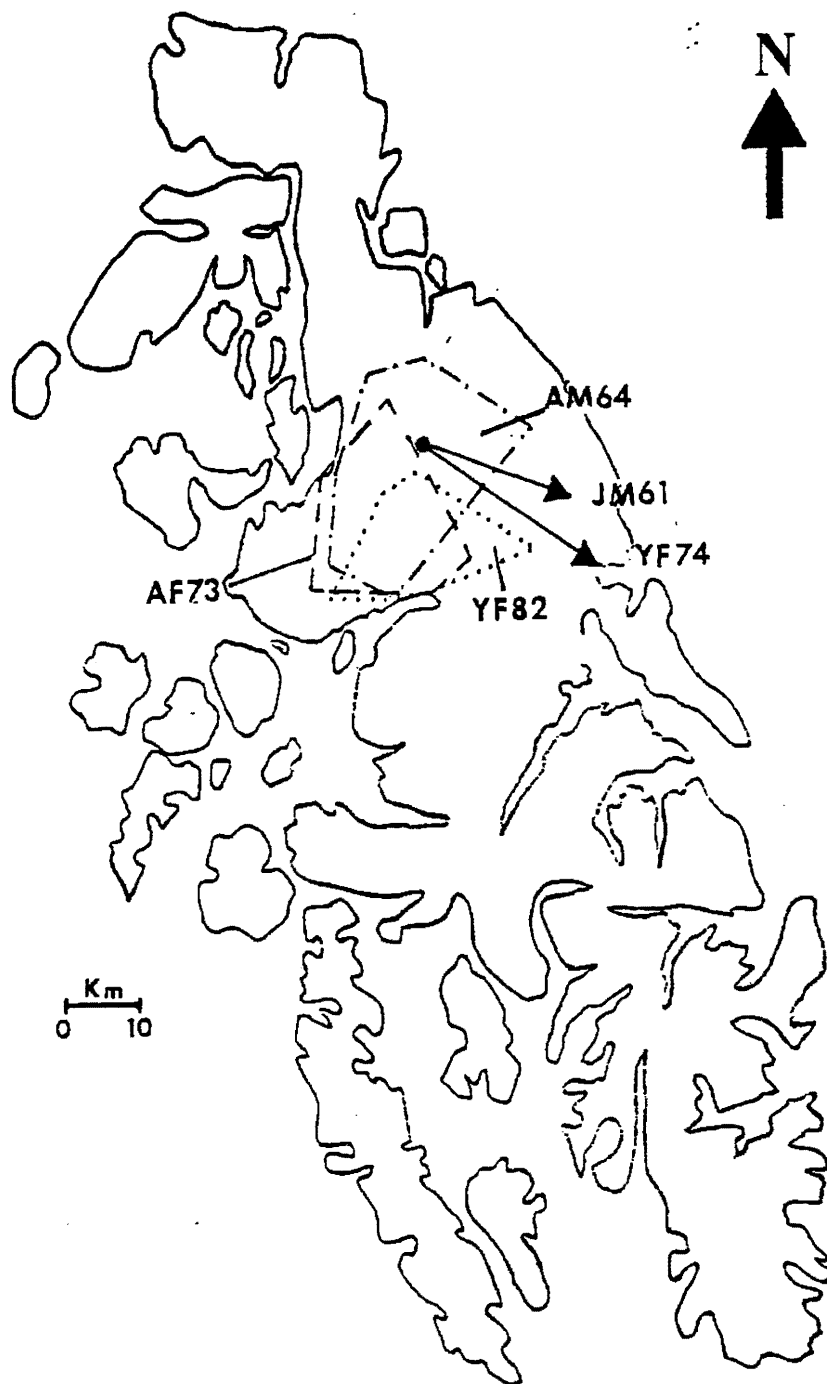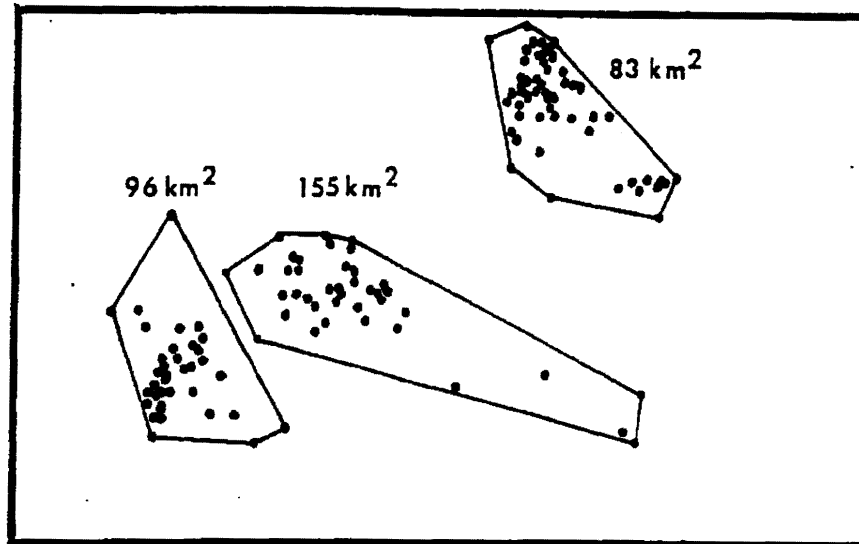
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Figure 10. Home ranges or movements of wolves exhibiting extraterritorial movements.
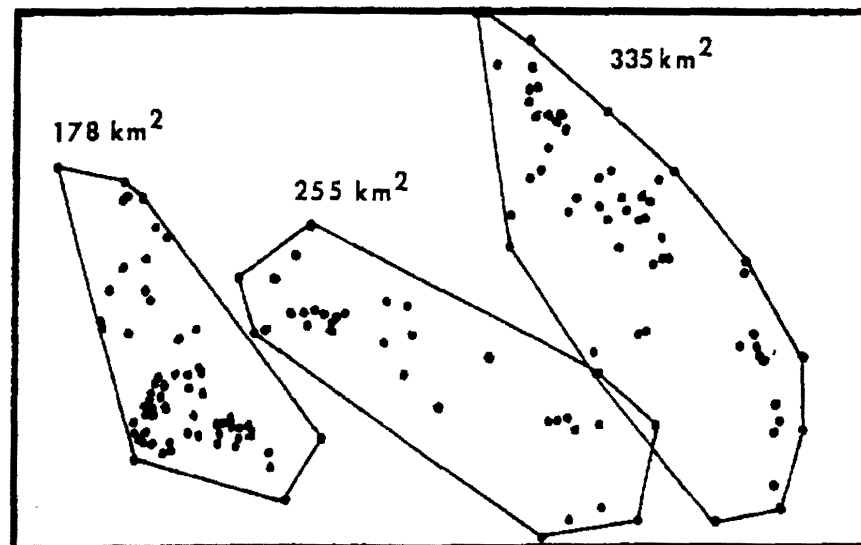
Denning

Nondenning

Figure 11. Home ranges for three wolf packs during the
denning (Apr 15 - Aug 1) and nondenning periods.

Although they may have abandoned the den according to the normal chronology of denning behavior, the wolves in this pack appear to have reduced their year-round activity in the entire valley within which the den was located. Analysis of telemetry locations show that prior to 27 July 1993, 23.9%, 35.8%, and 47.8% of the radiolocations for the pack were within 1000 m, 2000 m, and 3000 m of the den, respectively. After 1 August 1993, 3.1%, 10.6%, and 14.3% of the radiolocations for the pack were within 1000 m, 2000 m, and 3000 m of the den, respectively. The differences were all significant ($P < 0.0001$, $n = 228$) and suggest the possibility of a wide-scale disturbance affecting the activity of this pack.

Mortality.--Ten (41.7%) of 24 radio-collared wolves captured between March 1993 and November 1994 are known to be dead. Two more wolves were trapped but released unharmed after the trapper contacted us; therefore, these animals would normally have been mortalities, bringing the overall rate up to 50%. Ten (83.3%) of these mortalities (including those released unharmed) were due to hunting or trapping. Of the two nonhuman-related mortalities, one (YF82) was killed by a black bear, and the other died from unknown causes (the carcass couldn't be recovered). Using a Kaplan-Meier staggered entry procedure (Pollock et al. 1988), we estimated annual survivorship for wolves monitored between 1 June 1993 and 1 June 1994 to be 39% (95% C.I. = ± 22%, $n = 18$) (Fig. 12). The upper bound was only 61%, suggesting annual mortality exceeding 40%. Keith (1983) estimated the maximum per capita rate of increase (r) for wolves to be 0.35, which yields a finite rate of increase of 1.41. This suggests that unless wolves are reproducing at maximum rates on Prince of Wales Island, current mortality will precipitate a decline within at least a portion of the study area.

During the 1992-93 trapping and hunting seasons, 105 wolves from GMU 2 were killed and reported to the Alaska Department of Fish and Game. During the 1993-94 seasons, 103 wolves from GMU 2 were reported killed. Two (20%) of the 10 radio-collared wolves that were killed by hunters or trappers were shot illegally and would not have been reported. If this is representative of the annual human-related wolf kill, the harvests of 1992-93 and 1993-94 were probably closer to 130 animals. Given an estimated population of 300-330 wolves for Prince of Wales and Kosciusko Islands prior to the 1993-94 trapping season, and assuming that 90% of the harvest in GMU 2 occurs on these islands, we estimate that about 35-40% of the population is being harvested annually. A review of several studies of wolves in Alaska, Minnesota, and Canada revealed annual mortality not related to humans to average between 5 and 10% (Fuller 1989). If this mortality is added to the harvest rate, total annual mortality for 1993-94 was probably near 40 to 50%. This value falls well within the bounds of our estimated mortality for radio-collared wolves. In
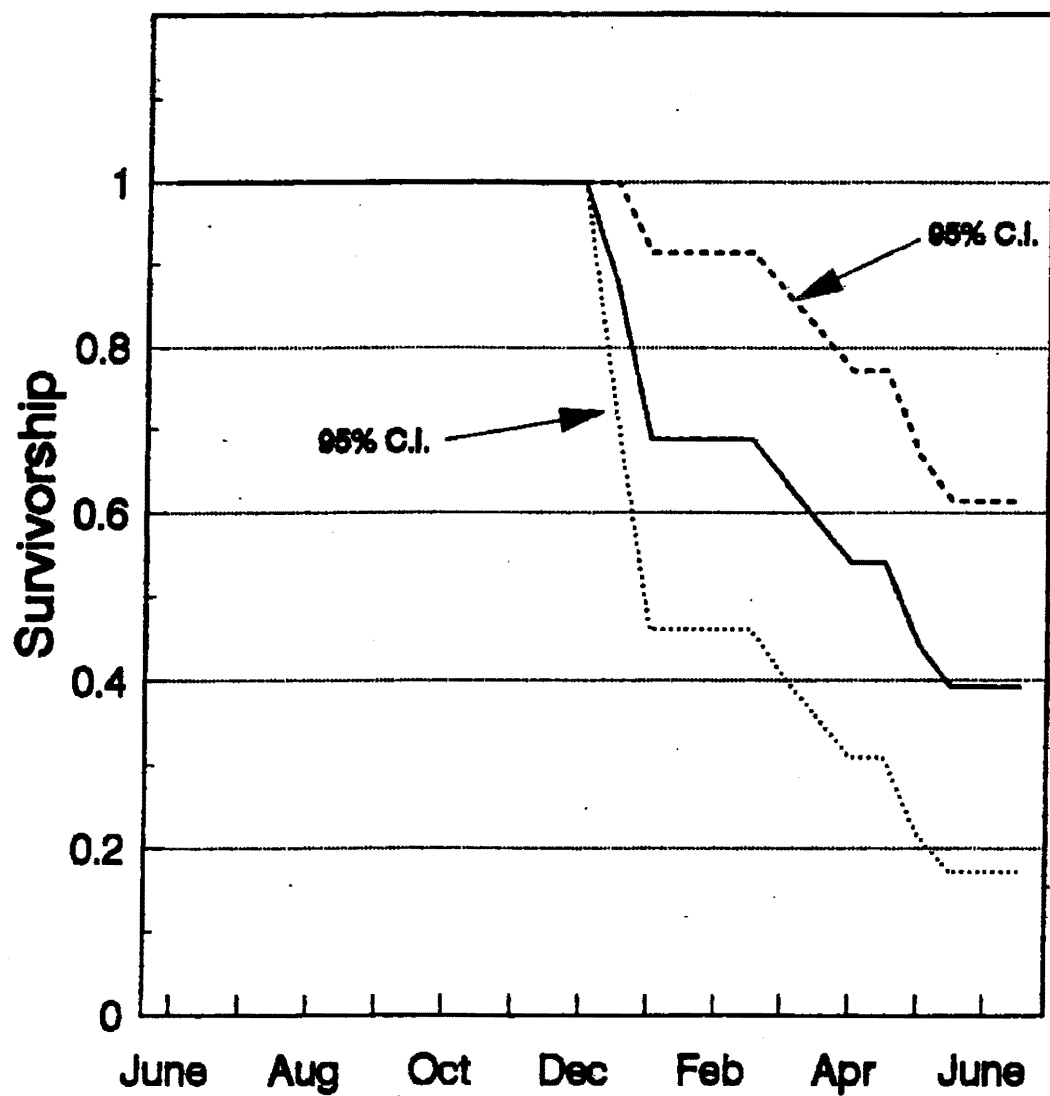
Figure 12. Survival function for wolves monitored between
1 June 1993 and 1 June 1994 on Prince of Wales and
Kosciusko Islands.

his review, Fuller (1989) also concluded that an annual harvest exceeding 28% would probably cause a population decline.

Seventy percent of the radio-collared wolves killed by humans were shot or trapped along or immediately adjacent to a road. Fuller (1989), Thiel (1978), and Mech et al. (1988) report that, because of human-caused mortality, wolves are absent from areas in which road density exceeds 0.6 to 0.7 km of road per km². In GMU 2, road densities in over 50% of the Wildlife Analysis Areas (WAAs) exceed this threshold (USFS GIS Database 1993). Although wolves currently inhabit all of these WAAs, their potential vulnerability to trapping and hunting is emphasized by these data.

Habitat Analysis.--For this report we defined habitat by 4 broad categories:

1) Noncommercial Forest (NC) - includes USFS volume classes ≤ 3 and muskegs
2) Low Volume Old Growth (LVOG) - includes USFS volume classes 4 and 5
3) High Volume Old Growth (HVOG) - includes USFS volume classes 6 and 7
4) Second Growth (SG) - includes new clearcuts and second growth regardless of age.

Finer resolution of habitat types is not warranted given the sample sizes used for analysis in this report.

We restricted our analysis to aerial radiolocations because location error was small (wolves were often directly observed) compared to the ground-based telemetry, and because habitat type could be unambiguously assigned, particularly with respect to logged versus unlogged types. Ground-based telemetry data will be analyzed for the final report by estimating the probability distribution of habitat within each error polygon. We determined that error in recording bearings is normally distributed about the true azimuth. Thus, the intersection of azimuths creates a multivariate normal distribution with the correlation estimated by the angular differences between bearings. We will select 30-50 random points that are bivariate normally distributed with a mean, variance, and correlation determined by the telemetry error of each radiolocation. These points will be plotted against habitat type maps to determine the probability distribution of habitat associated with each radiolocation. The habitat probability distributions of each location will be used to test for habitat use patterns with respect to microhabitat and landscape composition.

Although aerial locations have the advantage of easily assigning habitat type with minimal error, it must be emphasized that they represent habitat use only during daytime and primarily in good weather. Habitat availability was estimated by selecting approximately 150 random points within the pack home

ranges of each wolf analyzed. These points were overlaid on a timber inventory map produced from the USFS GIS database (1992). Analysis of habitat use versus availability used Chi-square tests of independence and Bonferroni confidence limits (Neu et al. 1974). Procedures were modified to account for error associated with estimation of habitat availability. Location data were analyzed for each wolf pack with sufficient aerial locations to enable statistical resolution.

Examination of all aerial location data showed that wolves were found in second-growth habitat only 7.2% of the time (95% C.I. = ± 3.4%, n = 227) (Fig. 13). Low-volume and high-volume old growth were used 46.8% (± 6.2%) and 9.5% (± 3.8%) of the time, respectively. Wolves were located in noncommercial forest habitat 34.7% (± 6.2%) of the time. Analysis of habitat use versus availability for 3 wolf packs with sufficient data indicated that use differed significantly from availability (Kosciusko pack - Chi-square = 14.81, P < 0.005, n = 45; Ratz Harbor pack - Chi-square = 8.25, P < 0.05, Chi-square = 43.5, P < 0.001, n = 37). All 3 packs used high-volume old growth habitat in proportion to its availability (Fig. 14). The Ratz Harbor and Kosciusko packs used low-volume stands more than expected and the Twin Spurs pack used noncommercial habitat more than expected (Fig. 14). All 3 packs used second-growth habitat significantly less than expected (Fig. 14). Two of the 3 packs were never located in second growth. For the pack with radiolocations within second growth, 4 of the 5 locations in second growth were of wolves at an estuary when salmon were spawning.

It should be emphasized that these data indicate selection at the stand level. Wolves occupy all landscapes present in GMU 2; however, they appear to be selecting unlogged habitat types within those landscapes at least during daytime. Independent confirmation of this comes from the analysis of the locations where scats were found along roads. Of 209 randomly collected scats, 63% (95% C. I = ± 6.5%) were located within 25 m of a leave strip or larger uncut patch, and 76% (± 5.8%) were found within 50 m (Fig 15). Over 60% (± 7.2%) of the scats were located along a road within the patch or leave strip.

Objective 3: Food Habits

Fecal analysis is being used to determine prey use by wolves. Scats have been collected from within the intensive study area as well as outside it. Scat analysis will be augmented by analysis of stable isotopes from hair and nail clippings of captured wolves to estimate the proportion of the diet that is marine in origin. Food habits data will eventually be compared to estimates of prey abundance by season and habitat composition.
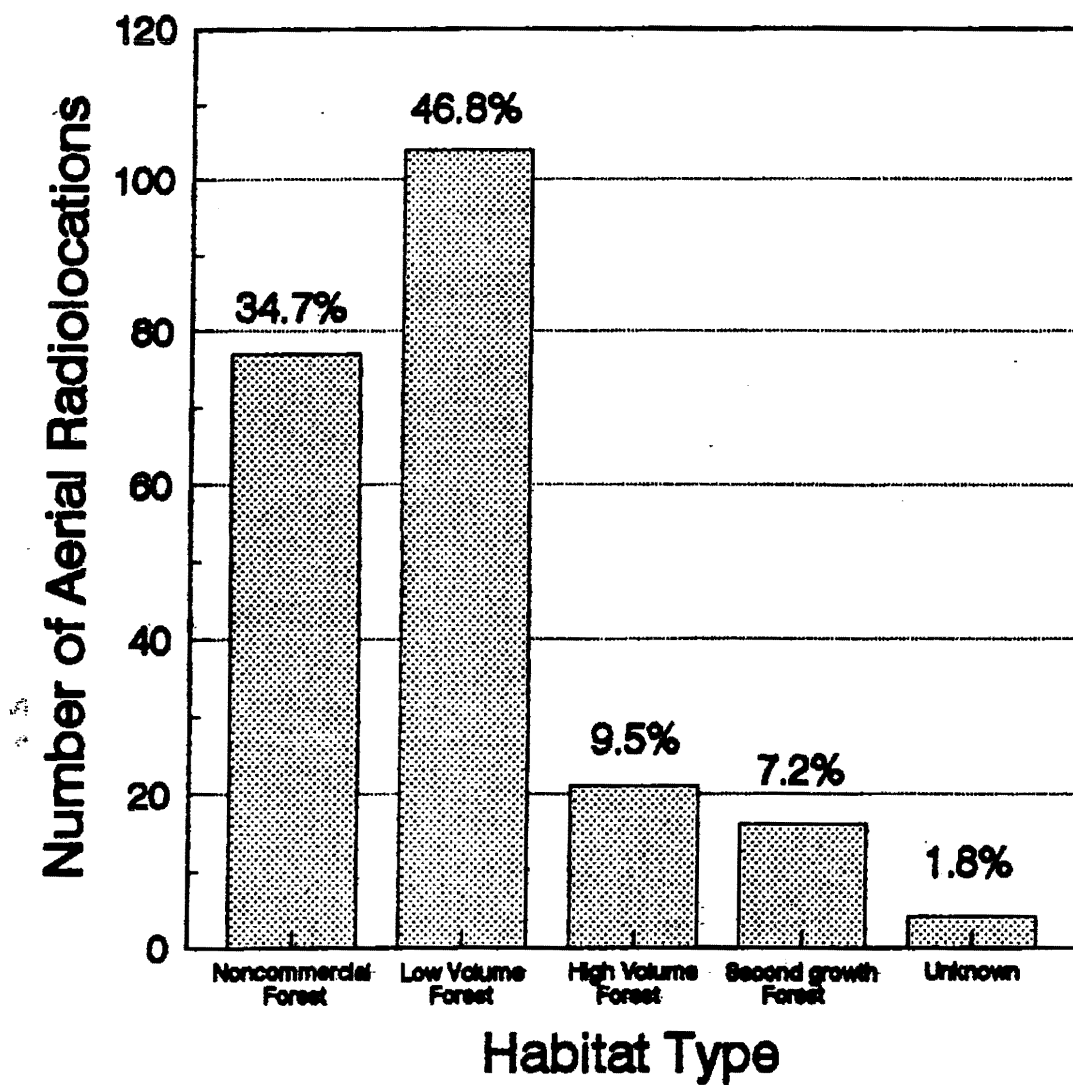
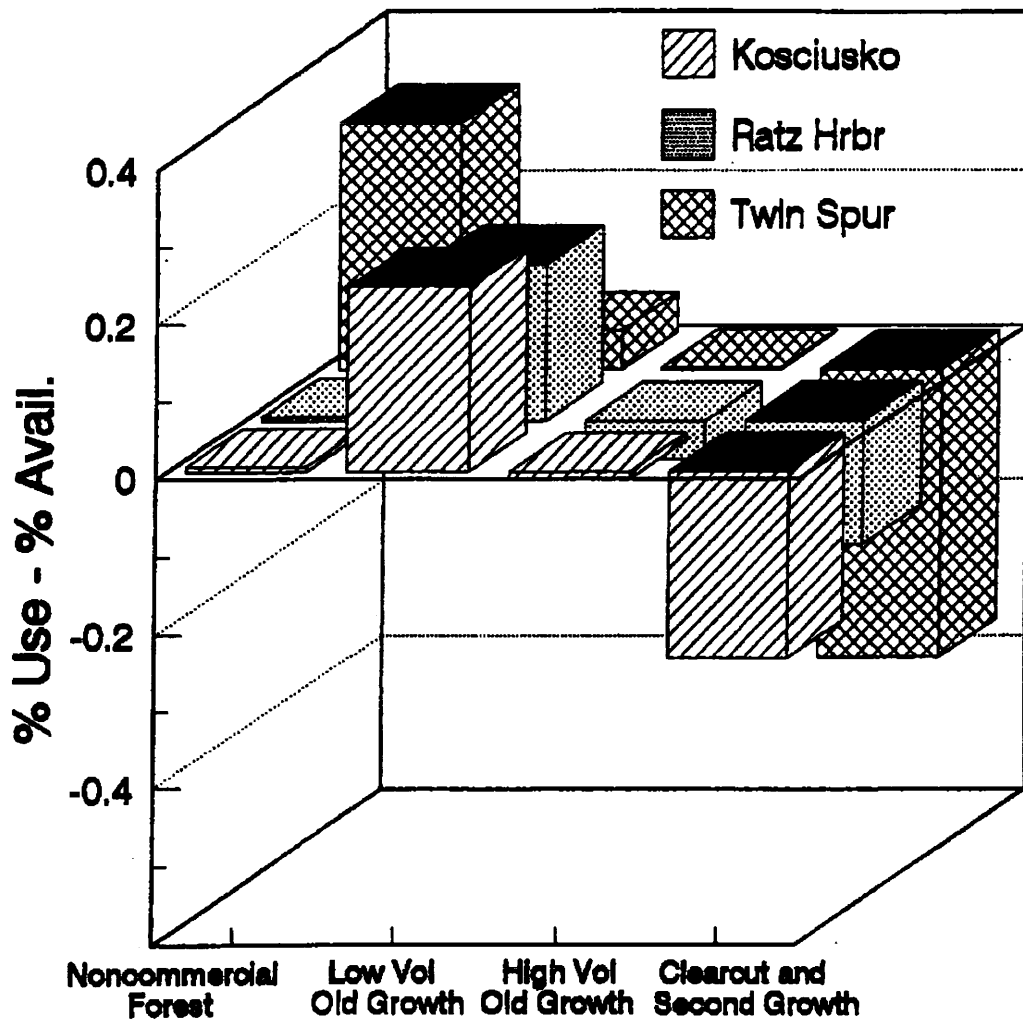Figure 13. Habitat use by wolves on Prince of Wales and Kosciusko Island.

Figure 14. Habitat use versus availability for three wolf packs on Prince of Wales Island. Graph shows difference between percentage of radio relocations (n = 124) within habitat type and percentage of habitat available within the pack home-range. Bars with solid black tops are different from zero (P < 0.05).
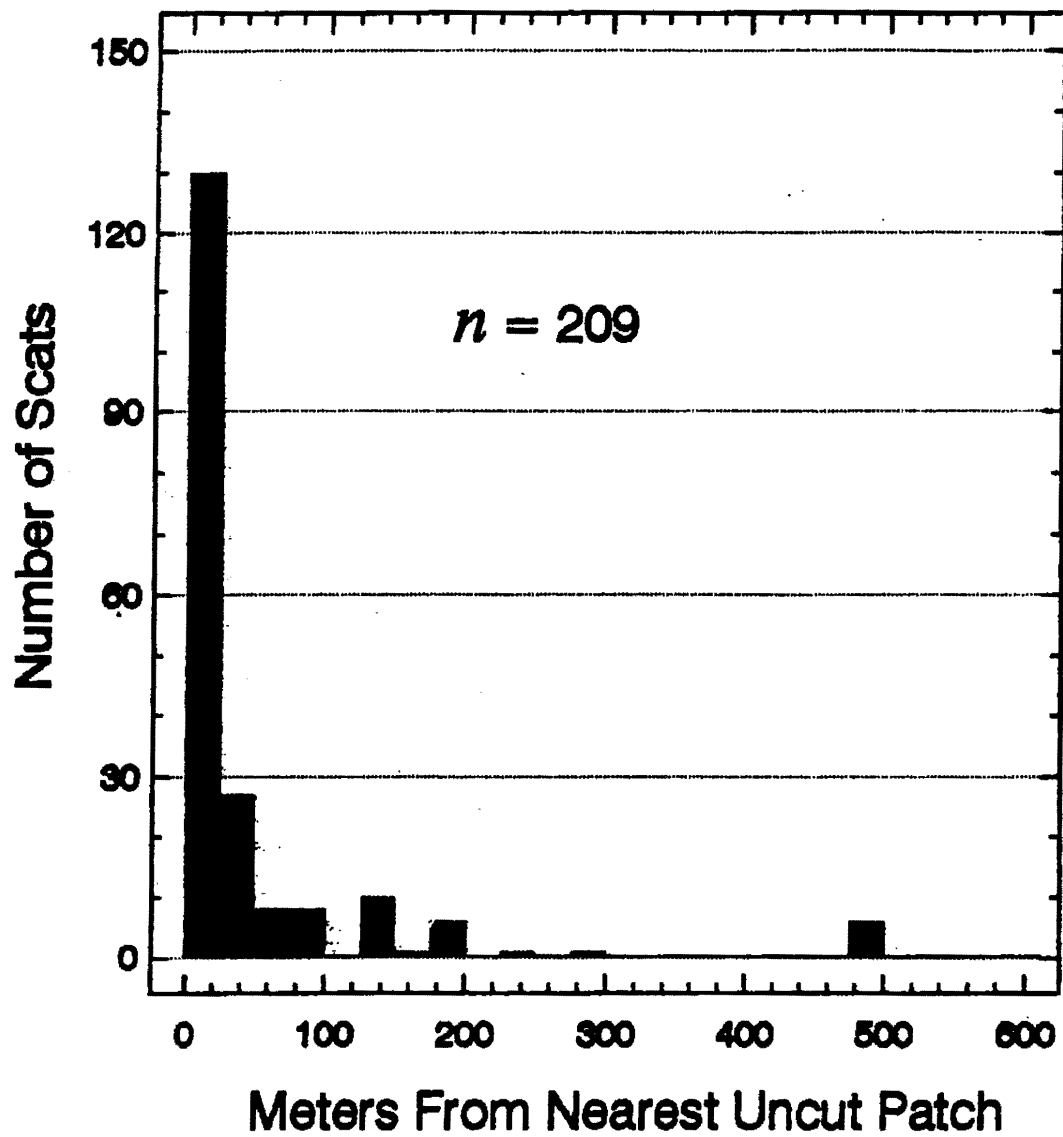
Figure 15. Distance of scats found along roads from nearest uncut patch.

<u>Results</u> <u>to</u> <u>Date</u>:

Thirty-seven deer carcasses were found that showed evidence of predation. Although most skeletons were incomplete, at least 7 were of adult males. Most carcasses were found in muskegs or along streams and lakes; however, 10 were found on roads.

We collected 316 scats between October 1992 and November 1994. Samples represent food habits during summer, fall, winter, and spring. A cursory examination indicates that 92% of scats contain deer hair. Beaver remains were observed in less than 6% of the scats. Fish scales or bones were found in 3% of the scats, and only during the months of August and September.

To date, 90 scats have been analyzed microscopically. Preliminary results show that the only species that occur in $\geq$ 10% of scats examined were deer (97%, 95 C.I. = ± 3.6%), beaver (36% ± 10.1%), and black bear (13% ± 7.1%) (Fig 16). Forty-two percent of the scats contained only deer remains, and no scats contained exclusively beaver. Beaver hair and bones were always found in conjunction with deer. One scat contained only black bear remains, but generally black bear hair occurred with other species. We have examined two adult bear carcasses that showed evidence of predation. Four of the 12 scats examined that contained bear remains were collected in winter, suggesting that wolves may prey on denning bears. Species with percent occurrence < 10% included mink, otter, wolf, ermine, marten, small rodents, birds, and fish. These data strongly indicate that deer is the primary prey species. Although beaver occurs in the diet year-round, it is only a supplement to a steady diet of deer.
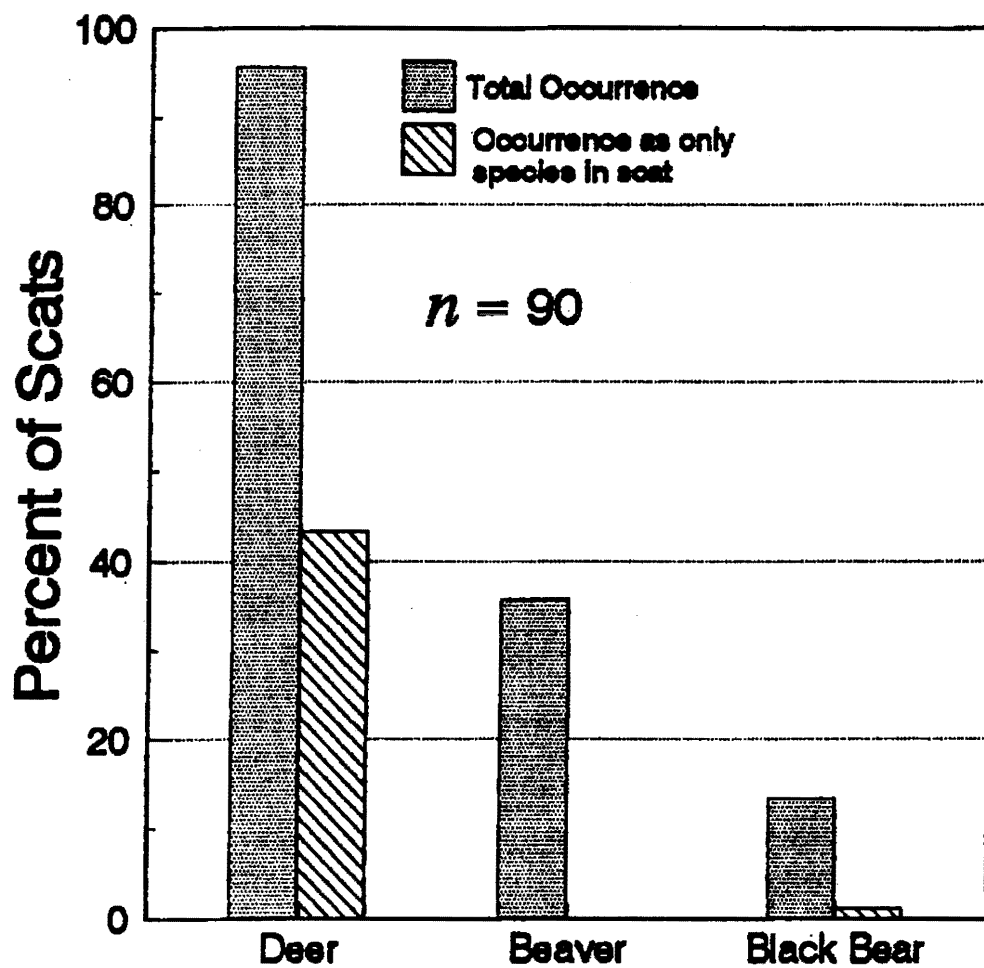
Figure 16. Percent occurrence of deer, beaver, and black
bear remains in scats collected on Prince of Wales and
Kosciusko Islands.

LITERATURE CITED

Andelt, W. F. 1985. Behavioral ecology of coyotes in South Texas. Wildl. Monogr. 94. 45pp.

Berg, W. E., and D. W. Kuehn. 1980. A study of the timber wolf population on the Chippewa National Forest. Minn. Wildl. Res. Ques. 40:1-16.

Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 in M. Bekoff, ed. Coyotes: biology, behavior, and management. Acad. Press, New York.

Friis, L. K. 1985. An investigation of subspecific relationships of the grey wolf, Canis lupus, in British Columbia. M.Sc. Thesis, Univ. of Victoria. 164pp.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105. 41pp.

Goldman, E. A. 1944. Classification of wolves. Part 2 in S. P. Young and E. A. Goldman, eds. The Wolves of North America, Dover Publications Inc., New York.

Hall, E. R. 1981. The mammals of North America. John Wiley and Sons, New York, N.Y. 1181pp.

Hanley, T. A. 1984. Relationship between Sitka black-tailed deer and their habitat. USDA Forest Service Gen. Tech. Rep. PNW 168. 21pp.

Hebert, D., J. Youds, R. Davies, H. Langin, D. Janz, and G. W. Smith. 1982. Preliminary investigations of the Vancouver Island wolf (C. l. crassodon) prey relationships. Pages 54-70 in F. H. Harrington and P. C. Paquet, eds., Wolves of the World. Noyes Publ., Park Ridge, NJ.

Keith, L. B. 1983. Population dynamics of wolves. Pages 66-77 in L. N. Carbyn, ed. Wolves of Canada and Alaska. Can. Wildl. Serv. Rep. Ser. 45. 135pp.

Kie, J. 1994. Program CALHOME. USFS. Pacific SW Forest Exp. Sta.

Klein, D. R. 1965. Postglacial distribution patterns of mammals in the southern coastal regions of Alaska. Proceedings, 14th Alaska Science Conference, August 29, 1963, Anchorage, AK.

Kolenosky, G. B. 1972. Wolf predation on wintering deer in east-central Ontario. J. Wildl. Manage. 36:357-369.

Mech, L. D. 1973. Wolf numbers in Superior National Forest of Minnesota. U.S. For. Serv. Res. Rep. NC-07. 10pp.

_____, S. H. Fritts, G. L. Radde, and W. J. Paul. 1988. Wolf distribution and road density in Minnesota. Wildl. Soc. Bull. 16:85-87.

Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. Can. J. Zool. 63:1068-1077.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.

Nowak, R. 1983. A perspective on the taxonomy of wolves in North America. Pages 10-19 in L. N. Carbyn ed., Wolves in Canada and Alaska. Can. Wildl. Serv. Rep. Ser. No. 45.

_____. 1994. Another look at wolf taxonomy. Proc. 2nd International Wolf Symposium, Edmonton, Alberta, Aug. 1992.

Packard, J. P., and L. D. Mech. 1980. Population regulation in wolves. Pages 135-150 in M. N. Cohen, R. S. Malpass, and H. G. Klein, eds. Biosocial Mechanisms of Population Regulation. Yale Univ. Press, New Haven, CT.

Pedersen, S. 1982. Geographical variation in Alaskan wolves. Pages 345-361 in F. H. Harrington and P. C. Paquet, eds. Wolves of the World: Perspectives of Behavior, Ecology, and Conservation. Noyes Publications, Park Ridge, NJ.

Person, D. K., and D. H. Hirth. 1991. Home range and habitat use of coyotes in a farm region of Vermont. J. Wildl. Manage. 55:433-441.

Person, D. K. 1988. Home range, activity, habitat use, and food habits of eastern coyotes in the Champlain Valley Region of Vermont. M.S. Thesis, Univ. Vermont, Burlington. 103pp.

37

Person, D. K. 1993. Ecology of the Alexander Archipelago wolf and responses to habitat change. Prog. Rep. No. 2., Alaska Dept. Fish and Game. 18pp.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. 88. 52pp.

Pimlott, D. H., J. A. Shannon, and G. B. Kolenosky. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ont. Dep. Lands and For. Res. Rep. Wildl. 87. 92pp.

Pollock, K. H., S. R. Winterstein, M. J. Conroy. 1988. Estimation and analysis of survival distributions for radio-tagged animals. Biometrics. 44:_____

Potvin, F. 1988. Wolf movements and population dynamics in Papineau-Labelle reserve, Quebec. Can. J. Zool. 66:1266-1273.

Schoen, J. W., and M. D. Kirchhoff. 1985. Seasonal distribution and home-range patterns of Sitka black-tailed deer on Admiralty Island, southeast Alaska. J. Wildl. Manage. 49:96-103.

Smith, C. A., R. E. Wood, L. Beier, and K. Bovee. 1987. Wolf-deer-habitat relationships in southeast Alaska. Fed. Aid. in Wildl. Rest. Rep. W-22-4, W-22-5, and W-22-6.

Thiel, R. P. 1985. The relationship between road densities and wolf habitat suitability in Wisconsin. Am. Midl. Nat. 113:404-407.

U.S. Forest Service. 1991. Tongass National Forest Draft Management Plan. USDA Forest Service.

U.S. Forest Service. 1993. A proposed strategy for maintaining well-distributed, viable populations of wildlife associated with old-growth forests in southeast Alaska. Interagency Comm. Rep. Juneau, AK. 278pp.

Van Ballenberghe, V., A. W. Erickson, and D. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildl. Monogr. 43. 43pp.

_____, and T. A. Hanley. 1984. Predation on deer in relation to old-growth forest management in southeastern Alaska. Pages 291-296 in W .R. Meehan, T. R. Merril, and T. A. Hanley, eds. Fish and Wildlife Relationships in old-growth forests. Amer. Inst. Fishery Res. Biol., Morehead City, NC.

38

Wallmo, O. C., and J. W. Schoen. 1980. Response of deer to secondary forest succession in southeast Alaska. For. Sci. 26:448-462.

Wood, R. 1990. Annual survey and inventory report - wolf. AK Dept. Fish and Game. Fed. Aid in Wildl. Rest. Rep.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.