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Ballard, Warren Baxter, Jr., Ph.D.

The University of Arizona, 1993

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DEMOGRAPHICS, MOVEMENTS, AND PREDATION RATES OF WOLVES IN NORTHWEST ALASKA

by

Warren Baxter Ballard, Jr.

A Dissertation Submitted to the Faculty of the

SCHOOL OF RENEWABLE NATURAL RESOURCES

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN WILDLIFE AND FISHERIES SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Warren Baxter Ballard, Jr.

entitled Demographics, Movements and Predation Rates of Wolves in Northwest Alaska

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy

Paul R. Krausman	11/30/93
Paul R. Krausman	Date
R. William Mannan	11/30/93
R. William Mannan	Date
O. Eugene Maughan	11/30/93
O. Eugene Maughan	Date
William W. Shaw	30 Nov 93
William W. Shaw	Date
Malcolm J. Zwolinski	11/30/93
Malcolm J. Zwolinski	Date

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

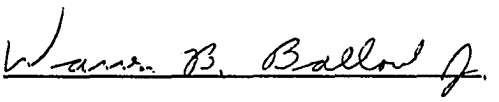
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ABSTRACT

During 1987 through 1992, 85 wolves (Canis lupus) were captured, radio-collared, and relocated from aircraft 1,123 times in northwest Alaska. Wolf packs usually did not follow migratory caribou (Rangifer tarandus) but maintained year-round resident territories that averaged 3,652 km^2. During years when caribou were absent and moose densities were low, $\leq$ 25% of the wolf packs moved 64 to 272 km to the caribou wintering grounds. Wolves used different slopes, aspects, and habitats in summer versus winter.

Twenty-five percent of the radio-collared wolves dispersed. Annual finite rates of increase ranged from 0.64 to 1.43. Annual wolf survival rates averaged 0.59. There were differences in survival rates among years. Sixty-one percent of the wolves died. Hunting was the main cause of death (69%) followed by rabies (21%). Rabies was a significant natural limiting factor. This wolf population could sustain mortality rates of about 53% annually.

Caribou and moose composed 51 and 42%, respectively, of the observed wolf prey. Adjusted for prey size, each pack killed 1 adult moose equivalent per 6.7 days. Wolf pack sizes and adjusted kill rates and kgs of available prey per wolf per day were correlated from several areas across North America. When caribou were present they were the principal prey. However, when caribou densities were <100/1,000 km^2

wolves preyed upon moose. Wolves preyed upon relatively healthy caribou and moose that were in marginal condition.

Wolves were killing about 6-7% of the caribou herd and from 11 to 14% of the moose population annually. Existing wolf predation may have serious impacts on resident, low-density moose populations.

During spring 1990 I tested the line-intercept method of sampling tracks for estimating wolf densities for a known wolf population (i.e., 48 wolves). The population estimate based upon line-intercept sampling was 50.7 (80% CI = 33.4 to 67.9) suggesting that the survey method provided relatively accurate population estimates.

I placed 23 satellite transmitters on wolves aged 10-months to 8 years with no apparent adverse effects on them. Accuracy of 1,855 relocations at 9 sites averaged 336 and 728 m for best and worst quality relocations, respectively. Satellite telemetry has potential for providing improved data sets for evaluation of wolf territory sizes and movements.

INTRODUCTION

The following chapters constitute partial fulfillment of the requirements for the degree of Doctor of Philosophy in Wildlife and Fisheries Science in the Graduate College at the University of Arizona. The chapters consist of six manuscripts that are intended for submission to peer-reviewed journals. Chapter 1 is the major portion of the dissertation and is intended for submission as a Wildlife Monograph. A number of techniques and methods had to be developed to complete the study. Chapters 2 through 6 represent the development of techniques and methods necessary to complete this research. As each chapter was completed they were submitted to various outlets. The chapters represent my ideas, analyses, and writing abilities. I designed the studies, collected most of the data, analyzed the data, and prepared the manuscripts. Each chapter has a number of coauthors. For co-authorship I used the guidelines provided by Dickson and Conner (1978) and the CBE style manual. Authorship of the chapters is as follows:

Chapter 1. Warren B. Ballard, Paul R. Krausman, Daniel J. Reed, and Steven G. Fancy.

Chapter 2. Warren B. Ballard, Mark E. McNay, Craig L. Gardner, and Daniel J. Reed.

Chapter 3. Warren B. Ballard, Daniel J. Reed, Steven G. Fancy, and Paul R. Krausman.

Chapter 4. Steven G. Fancy and Warren B. Ballard.

Chapter 5. Warren B. Ballard, Gary M. Matson, and Paul R. Krausman.

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Dickson, J. G., and R. N. Conner. 1978. Guidelines for authorship of scientific articles. Wildl. Soc. Bull. 6:260-261.

CHAPTER 1

WOLF DEMOGRAPHICS AND PREDATION ON CARIBOU FROM THE WESTERN ARCTIC HERD, NORTHWEST ALASKA

Abstract: We studied wolf demographics, movement patterns, and predation characteristics in relation to a migratory caribou population in northwest Alaska. We wanted to determine if wolves were migrating with the caribou and to quantify the effects of wolf predation on caribou of the Western Arctic Herd. During 1987 through 1992, we captured 85 wolves (Canis lupus) within 19 packs in northwest Alaska. Wolves were radio-collared, and relocated from fixed-wing aircraft on 1,123 occasions. Pup sex ratios at capture indicated more females than males (183:100), whereas yearling sex ratios were equal. Adult sex ratios were biased towards males (192:100) partially due to selection of alpha males for capture. Wolf packs usually did not follow migratory caribou (Rangifer tarandus) but maintained year-round resident territories that averaged 3,652 km^2. Large packs had larger territories than did small packs (r = 0.89). During years when caribou were absent and moose densities were low, up to 25% of the radio-marked wolf packs followed migratory caribou to winter range and then returned to their original territory for denning. We speculate that wolves historically (before 1950) preyed primarily on caribou and migrated with them to their wintering areas. We

further speculate that establishment of resident moose (Alces alces) populations within northwest Alaska during the past 40 years has altered that migratory behavior.
Some radio-collared wolves (n = 22) dispersed during the study. The sex ratio of dispersers did not differ significantly from 50:50 and there were no differences ($P < 0.05$) in mean ages or percent yearlings between sexes. Dispersal was most prevalent during April through July. Spring wolf densities within the study area increased from 2.7 to 4.4 wolves/1,000 km^2 during 1987 through 1990 and then declined to 1.5 wolves/1,000 km^2 following a rabies epizootic. Annual finite rates of increase ranged from 0.64 to 1.43.

Habitat use by wolves differed between summer and winter. We observed wolves on kills less frequently during summer than during winter. This was probably due to dense foliage during summer, while during winter there was complete snow cover and more intensive tracking efforts. Wolves were found at relatively high elevations (≥230 m) during winter and spring. Lower elevations were used during summer and December (≤139 m). All denning wolves were regularly attending den sites by the third week of May. Pup litter sizes averaged 5.3 ± 2.0. Annual wolf survival rates averaged 0.59. Significant ($P < 0.05$) differences in annual survival resulted from a rabies epizootic in 1990.

Most of the wolves (n = 52) that we radio-collared (n = 85) died during the study. Hunting was the main cause of death (69%) followed by rabies (21%). Most (63%) mortality occurred during December through March when snow cover permitted wolf hunting from snow machines. Rabies was a significant natural limiting factor of this wolf population (i.e., 21% of all mortality). About 64% of rabies-caused mortality occurred during May and June. Comparisons of overwinter mortality in relation to exponential rates of increase within individual wolf packs suggested that this wolf population could sustain an annual mortality from all causes of about 53%.

Caribou and moose composed 51 and 42%, respectively, of the kills observed during the study. Several wolf packs were relocated daily during March and April 1988-1990 to estimate predation rates. Overall, adult caribou and adult moose composed 41 and 36% of the kills, respectively. Adjusted for prey size, each pack killed 1 adult moose equivalent (400 kg)/6.7 days. Most kills were consumed ≥90%. Wolf pack sizes, adjusted kill rates, and kgs of available prey/wolf/day were significantly correlated ($P < 0.001$) in several areas across North America where caribou and moose were the principal prey species. When caribou were present within areas used by individual wolf packs they were the principal prey. However, when caribou densities

were <100/1,000 km^2 wolves preyed on resident moose. Based upon marrow fat analyses, wolves were preying on relatively healthy caribou during winter while moose killed were in less than optimum condition.

We estimated that wolves within the range of the Western Arctic Caribou Herd were killing 6-7% of the caribou annually. Caribou left wolf pack territories during winter and wolves switched to preying on moose for 4 months. We estimated that wolves were killing from 11 to 14% of the moose population annually. Wolf densities were limited by hunting and trapping, and wolf predation at present levels had little effect on caribou of the Western Arctic Herd. However, existing wolf populations may have serious impacts on local, low-density moose populations that have become established during the past 40 years.

INTRODUCTION

The Western Arctic Caribou (Rangifer tarandus granti) Herd (WACH) has historically been 1 of the largest caribou herds in North America and is the largest herd in Alaska. The herd is an important resource for subsistence and recreation. The herd was thought to number between 200,000 and 300,000 individuals during the 1950s and 1960s, but declined in the 1970s (1976) to a low of about 75,000. Several factors caused the decline (Davis et al. 1980); excessive human harvests and wolf predation were the primary factors (Doerr 1979, Davis and Valkenburg 1985).

Following the low in 1976, the caribou population increased in response to reduced human harvests, mild winters, and apparently reduced predation by wolves (Davis and Valkenburg 1985). If Davis et al.'s (1980) 1976 population estimate of 75,000 caribou was accurate, the WACH increased at an annual finite rate of increase of 1.12 (r = 0.11) between 1976 and 1991 (n = 417,000; Fig.1). Davis et al. (1980) and Davis and Valkenburg (1985) described the recent history of the Western Arctic Caribou Herd. In 1984 the Alaska Board of Game approved a WACH management plan that stated that the highest management priority is to prevent the herd from declining to low numbers (Alas. Dep. Fish and Game 1984). To avoid future catastrophic declines in the caribou herd, it is imperative that caribou harvests

and wolf and caribou population levels be routinely monitored.

Historical abundance of wolves in northwest Alaska is poorly understood. As in most areas of Alaska during the late 1940s and early 1950s, the Federal government used poison and aerial shooting to reduce wolf populations (Kelly 1954). Several estimates of wolf numbers in northwest Alaska have been made since the early 1950s, but their accuracy is unknown. R.O. Stephenson (Alas. Dep. Fish and Game, unpubl. data) estimated wolf density at 6/1,000 km^2 ($\underline{N}$ = 720 wolves) in 1977, while in 1981 Quimby (1982) estimated the density at 6/1,000 km^2 for 85% of the area and 1.9 to 2.6 wolves per 1,000 km^2 for 15% of the area ($\underline{N}$ = 476 wolves). Wolf densities within our study area were estimated at 12.9/1,000 km^2 in spring 1977 (Davis and Valkenburg 1981). James (1983) thought that the wolf population was increasing in 1981-82 and predicted a significant increase in future years as the caribou population continued to increase. Although the WACH increased rapidly during the 1980s, wolf numbers did not appear to respond to increased prey. Lack of population response and reported low numbers of wolves by members of the public (James 1984, Larsen and James 1987) created interest in determining the exact status of the wolf population. Consequently, we initiated a study during

spring 1987 to determine the status of the wolf population and its relationship to the WACH. Our objectives were to describe the demographics, movement patterns, and diet of wolves in relation to migratory movements of caribou in northwest Alaska.

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STUDY AREA

Davis et al. (1980) defined the range of the WACH as encompassing 362,600 km^2 in northwest Alaska (Fig. 2). During spring 1987 we selected an area that appeared representative of caribou winter range as the core study area for the wolf project (Fig. 3).

The core area was approximately 12,279 km^2 and included the eastern half of Kobuk Valley National Park, the eastern two-thirds of Selawik National Wildlife Refuge, and northern portions of Koyukuk National Wildlife Refuge, and was contained largely within Game Management Unit (GMU) 23 (approx 119,140 km^2). We refer to GMU 23 as northwest Alaska.

Topography was varied with broad, relatively flat plains along the major river systems grading into rolling hills such as the Waring Mountains to rugged steep mountainous terrain in the major mountain ranges such as the Purcell and Baird Mountains. Elevations within the study area ranged from near sea level along the Kobuk and Selawik rivers to 1,168-1231 m for several mountain peaks that rise abruptly from valley floors.

Vegetation of the area was diverse ranging from unvegetated sand dunes (largest being the Greater and Little Kobuk sand dunes), gravel bars, rock screes, lakes and ponds of various sizes, wetlands, and marshes grading into dense

tall white spruce (Picea glauca) forests along major river systems. Willows (Salix spp.), which provide browse for ungulates, occur throughout the study area but are most common along riparian areas and least common in open tundra. Away from major river systems, the area included sparse to dense taiga scrub forests of white and black spruce (Picea merino) that grade into or contain alpine and arctic tundra. Small tundra lakes and wetlands were prominent along the Selawik River. The area contained portions of the Kobuk, Selawik, and Huslia river systems.

The area had a maritime climate during ice-free periods and long cold periods during winter months (United States Department of Interior 1987). Temperature extremes ranged from 32 C to -51 C. Summer temperatures averaged about 16 C whereas winter temperatures of -7 to -34 C were common along with extreme wind chill factors. Annual precipitation averaged 6-8 cm in lowlands and $\leq$ 12 cm in upland areas. Half of the rainfall occurred during July and August. Winter winds often resulted in hardpacked snow and large drifted areas. Because of severe winter winds, snow depths ranged from 0 m in upland windblown areas to several meters in low riparian areas.

Mammals common to the study area include brown (Ursus arctos) and black bear (Ursus americanus), wolverine (Gulo gulo), lynx (Felis lynx), beaver (Castor canadensis),

muskrat (Ondatra zibethicus), river otter (Lutra canadensis), mink (Mustela vison), marten (Martes americana), red fox (Vulpes vulpes), and arctic fox (Alopex lagopus). In addition to caribou, other potential prey species for wolves include moose, Dall's sheep (Ovis dalli) muskoxen (Ovibos moschatus), snowshoe hare (Lepus americanus), and several species of squirrels and microtine rodents.

Moose did not occur within the Selawik National Wildlife Refuge area until the early 1950s when they were first observed in the Tagagawik River area (United States Department of Interior 1987). During late winter, moose distribution appears restricted to narrow fringes of riparian habitats along major rivers and streams. During autumn, moose are more widely distributed with relatively high densities occurring along the northern Purcell Mountains and the Tagagawik Hills area. D. N. Larsen (Alas. Dep. Fish and Game, pers. commun.) estimated overall autumn density of moose on the refuge at 166/1,000 km^2. Moose densities in small quadrant sample areas ranged from 27 moose/1,000 km^2 to 811 moose/1,000 km^2 during autumn 1985.

METHODS

We used acceptable field methods (American Society of Mammologists 1987) while conducting our research. We located wolves for capture usually during March or April after fresh snowfall of ≥ 8 cm. Fixed-wing aircraft (Piper PA-18) with experienced pilot-observer teams searched lake shores, ridgelines, streams, and other likely travel routes for wolf tracks. Tracks were followed until wolves were found. Once spotted, wolves were captured for radio-collaring using helicopter darting procedures similar to those described by Ballard et al. (1982). Wolves were immobilized with etorphine hydrochloride (HCL) (M-99, D-M Pharmaceuticals, Inc., Rockville, Maryland) or with a combination of tiletamine hydrochloride and zolazepam hydrochloride Telazol, (A. H. Robins Company, Richmond, Va.). Etorphine HCL was available in a concentration of 1 mg/mL and was administered to wolves of all sex and age classes at a dose of 2.5 mL. After processing, each wolf was administered the antagonist diprenorphine HCL (M-50-50, D-M Pharmaceuticals, Inc., Rockville, Md.) in an equivalent dose but at a concentration of 2 mg/mL. Induction and immobilization times were identical to those reported by Ballard et al. (1982).

Telazol was available in 500 mg vials. We recombined 2 vials of the drug with 5 mL of sterile water resulting in a

concentration of 200 mg/mL. All wolves were immobilized with a dose of 2 mL (Ballard et al. 1991). Each immobilized wolf was sexed, aged to the nearest month based on tooth eruption and wear assuming a 1 June birthdate, weighed, measured, ear tagged, blood sampled, and equipped with a conventional VHF transmitter or a satellite UHF transmitter (both manufactured by Telonics, Inc., Mesa, Ariz.).

We attempted to relocate instrumented wolf packs within the core study area approximately once every 2 weeks throughout the year except during specified periods. During March and April 1988 through 1990, radio-marked wolf packs were relocated daily to estimate prey species killed and kill rates of various sized wolf packs. We rated availability of caribou as prey during March and April based upon the proportion of radio-collared caribou from the WACH located within the wolf study area and by qualitative observations made during the study.

We monitored birth and survival of wolf pups annually based on counts at den sites and comparisons of counts during early autumn, mid-winter, and late spring. Ages of wolves observed, but not handled, were estimated from relative size and other criteria described by Jordan et al. (cited by Mech 1970).

We estimated total territory sizes from all relocations excluding obvious extraterritorial forays, dispersals, and

migratory movements using the minimum convex polygon method (Mohr 1947). We used the McPAAL software package (M. Stuwe and C. E. Blohowiak, Conservation Research Center, National Zoological Park, Smithsonian Institution, Front Royale, Va., 1985) to estimate territory sizes. We defined winter as the period from 1 October through 30 April and summer from 1 May through 30 September. At each wolf relocation we recorded the date, time, number, sex and age of associates, activity, and type of habitat on standardized forms. Vegetation was classified within one full turn of the aircraft, using classifications of vegetation described by Viereck and Dyrness (1980). We determined slope, aspect, and elevation at each relocation from 1:63,360-scale topographic maps after each flight. We determined elevation by extrapolating between contour lines to the nearest 15 m interval. We classified slopes into categories using contour line intervals: flat = <10°; gentle = 11-30°; moderate = 31-45°; and steep = >45°. Aspect was classified as 1 of 8 compass directions or as flat, gully, or ridge from a line perpendicular to the contour lines through the relocation point.

We classified wolf movements into four categories: (1) resident - wolves remained within annual territory boundaries, (2) extra-territorial forays - usually single wolves which temporarily left observed territories for

varying time periods and distances but returned to the original territory, (3) dispersal - single wolves which permanently left their original territory and did not return (the latter two types of movements were non-directional and did not appear related to movements of prey species), and (4) migratory - entire packs left observed territory boundaries during winter in same direction as migratory caribou and then returned to original territory for denning. We classified a wolf as missing when we could no longer relocate it and its fate was unknown. Seasonal shifts in territory use occurred when wolf packs made movements away from core areas within their territory but remained within the territory boundaries.

Spring and autumn wolf densities within the core study area were estimated based on known numbers of wolves within radio-marked packs. These estimates were extrapolated to other portions of GMU 23 and other areas within the range of the WACH, if appropriate, for estimation of wolf numbers. These methods follow those used by Ballard et al. (1987) and recommended by Fuller and Snow (1988). To verify whether study area density estimates could or should be extrapolated to additional areas we conducted periodic surveys using Stephenson's (1978) track count method in areas where few or no radio-collared wolves existed. The wolf population was assumed to be composed of 10% lone or single wolves

(Stephenson 1978, Ballard et al. 1987, Fuller and Snow 1987).

We classified carcasses of ungulates observed while relocating instrumented wolf packs by cause of death based on criteria described by Stephenson and Johnson (1972) 1973), Peterson (1977), Peterson et al. (1984), Ballard et al. (1987), and Fuller (1989). Cause of death was classified as wolf-killed, bear-killed, hunter-killed, scavenged, winter-killed (starvation), or unknown. We sexed and aged wolf-killed ungulate carcasses from fixed-wing aircraft by presence and/or shape of antlers, presence of vulva patch, body size, and pelage (Peterson 1955, Skoog 1968, Ballard et al. 1987). We aged wolf-killed calf and yearling moose and caribou to the nearest month by assuming that parturition occurred during May and June, respectively (Ballard et al. 1987). When practical, we examined ungulate carcasses in situ to confirm cause of death and to examine carcasses for obvious physical abnormalities. We collected mandibles and longbones for determining percent marrow fat (Neiland 1970) and prey age (Sergeant and Pimlott 1959, Skoog 1968). Survival rates of radio-collared individuals were determined using Kaplan-Meier procedures (Pollock et al. 1989). The major advantage of this method is that, when radio contact is lost with an animal and its fate is unknown, it can be censored from the data set. The

procedure is simple, flexible and allows staggered entry of tagged animals during the study (Pollock et al. 1989).

Comparisons of means were conducted with Mann-Whitney U tests and Kruskal-Wallis ANOVA (Ott 1988). Frequency data were compared by Chi-square tests. Wolf weights were compared with Tukey's test (Sokal and Rohlf 1969:238). Correlations between pack sizes and territory sizes, time at kills, kill rates, and prey weight/wolf/day were analyzed with Spearman's rank correlation r_s (Conover 1971) with significance based upon the t-distribution (n - 2 df). For illustrative purposes, we used linear regression models to depict relationships for significant Spearman rank correlations. We compared survival rates by t-test (Pollock et al. 1989). Unless stated otherwise, $P \leq 0.05$ was necessary for significance. Parameter estimates are presented as point estimates $\pm$ 1 standard deviation.

RESULTS AND DISCUSSION

Capture and Telemetry

We captured and radio-collared 86 wolves in northwest Alaska during April 1987 through April 1991 (Table 1). No wolves were killed as a result of immobilization, but 1 wolf was killed for rabies testing because it bit one of the tagging personnel. We captured wolves 102 times: 72 wolves were captured once, 12 were captured twice, and 2 were captured three times (Table 1). The drug combination of tiletamine HCL and zolazepam HCL was effective and safe for immobilizing wolves by helicopter darting (Ballard et al. 1991).

Sex and age composition of wolves at initial capture was 12 male pups, 22 female pups, 7 male yearlings, 7 female yearlings, 25 adult males, and 13 adult females. Overall, pup sex ratios favored females (183:100) ($\underline{X}^2 = 2.9$, $\underline{P} = 0.09$), while yearling sex ratios were 50:50 ($\underline{X}^2 = 0.0$, $\underline{P} = 1.0$). Adult sex ratios were biased towards males (192:100) ($\underline{X}^2 = 3.8$, $\underline{P} = 0.05$). The latter ratio was biased because of our tendency to attempt capture of large alpha males. Overall, pooled sex ratios were not different from 50:50 ($\underline{X}^2 = 0.05$, $\underline{P} = 0.83$).

Sex ratios differ by geographic area depending on a number of factors. Cowan (1947), Stenlund, (1955), Rausch (1967), Mech (1975), Nielsen (1977), and Parker and Luttich

(1986) reported sex ratios favoring males whereas Hayes et al. (1991) reported a sex ratio favoring females. Hayes et al. (1991) suggested that, if food shortages were responsible for sex ratios favoring males as Mech (1975) suggested, a sex ratio favored by females may indicate that food was not limiting.

Pups are typically more vulnerable to hunting and trapping mortality than adults (Van Ballenberghe et al. 1975, Ballard et al. 1987). Sex ratios in the harvest favored males (see Hunting and Trapping) which may account for the skewed pup sex ratio in the population. Differences in sex ratios in this study between pups and yearlings suggest that females have lower survival than do males during their first year, but survival rates estimates were not different between the two sexes (see Survival).

Adult males had a mean weight of 47.2 kg and were the heaviest sex-age class examined (Table 2). Weights of male pups and yearlings were similar to those of adult males, indicating that male wolves attained most of their weight by 11 months of age. Female pups were significantly lighter than all other sex-age classes (Table 2). By 23 months of age, yearling females attained adult female weights. Males were significantly heavier than females for each age class.

Territory Sizes and Movements

During April 1987 through July 1992, 85 radio-collared wolves within 19 wolf packs were relocated from fixed-wing aircraft on 1,123 occasions (Table 3). Total relocations/pack averaged 62 ± 61 (range = 6-209). Length of radio contact with each pack averaged 736 ± 539 days (Fig. 4). Each pack was relocated an average of 1/22.4 ± 13.9 days.

Several investigators have examined the number of relocations necessary to adequately describe wolf territory size. Fritts and Mech (1981) determined that an average of 79 relocations was necessary when packs were located ≤1.5 years in Minnesota. Messier (1985) suggested that year-long territories were defined after 40-80 daily relocations, while Carbyn (1983) and Fuller and Snow (1988) determined that about 30 relocations were necessary to describe 85-90% of total territory size. Ballard et al. (1987) estimated that approximately 60 relocations were required to adequately define territory sizes in south-central Alaska where territory sizes were commonly >1,500 km^2. Based upon the above criteria but eliminating dispersals, extra-territorial forays, and migratory movements, many packs listed in Table 3 may not have been relocated frequently enough to accurately estimate either seasonal or total territory sizes. For assessing territory sizes we assumed that seasonal and total territory sizes were adequately

defined when numbers of relocations were >20 and >78, respectively. Using these criteria, seven packs were relocated frequently enough to estimate seasonal and total territory sizes.

Total territory size (excluding long-distance movements, dispersals, and migratory movements) for 7 wolf packs relocated an average of 124 ± 45.5 times each during the study averaged 3,652 ± 1,955 km^2 (Table 4). These intensively studied packs were relocated an average of once/ 11.4 ± 4.5 days. These territories were the largest reported for wolves in North America (Ballard et al. 1987). Winter and summer territories averaged 2,587 and 1,897 km^2, respectively, and were significantly correlated (r_s = 0.86, P = 0.01). Winter territory sizes were not significantly different from summer territory sizes (Z = 1.18, P = 0.24); lack of significance appeared due to the Nuna Creek pack that had a large summer range in relation to its winter range (Table 4). Widespread movements associated with several wolves which subsequently succumbed to rabies during summers 1990 and 1991 may have been partially responsible for the relatively large summer territory. Excluding the Nuna Creek pack, winter territories were significantly larger (Z = 2.20, P = 0.03) than summer territories. Both Fuller (1989) and Hayes et al. (1991) found no differences in summer versus winter territory sizes. We attribute our

findings to the large differences in prey densities and denning behavior between winter and summer (see Feeding Ecology). Relatively low prey densities during winter caused wolves to range over large areas to find vulnerable prey. Caribou and moose were available during summer within each pack territory, and the radius from the den site may have limited the distances that wolves could effectively hunt and still feed pups.

Peterson et al. (1984), Ballard et al. (1987), Fuller (1989), and Hayes et al. (1991) found correlations between pack size and territory size. In our study, early winter maximum pack size was correlated with summer (r_s = 0.96, P = 0.0005), winter (r_s = 0.71, P = 0.07), and total territory size (r_s = 0.89, P = 0.007), respectively.

We expected that most wolves within the study area would follow migratory caribou between summer and winter ranges. However, plots of convex polygons excluding extra-territorial forays, dispersals, and migratory movements suggested that most wolf packs in northwest Alaska were territorial and nonmigratory (Fig. 5). Overlap among territory boundaries (Fig. 5) was the result of using convex polygons and plotting total territory areas for the entire study period. Although some territory overlap occurred (particularly along territory edges) packs used these areas in different seasons. Several new packs became established

in areas where packs were eliminated or greatly reduced in size because of mortality. The latter included establishment of the Dunes pack within the Rabbit Mountain area and establishment of the Selawik River pack within the Kiliovilik territory (Fig. 5).

Some packs occasionally followed migratory caribou to winter range, apparently when prey densities reached low levels. We documented 2 cases in 1989 and 1 each in 1990 and 1991 of wolf packs that left resident territories and followed caribou to winter range but then returned to the original territory for denning (Table 5). In all cases, these movements occurred during winters when relatively few caribou wintered within wolf territories. Wolves apparently were forced to migrate after caribou left their pack area. We suspect they moved because moose densities were not high enough to sustain the packs. Wolf migration was not predictable and varied annually. Overall, about 11% of the radio-marked packs annually migrated with caribou. The percentage of packs that migrated annually was as follows: 0% during 1987-88 [b = 0 of 5], 25% during 1988-89 ($\underline{n}$ = 2 of 8), 8% during 1989-90 ($\underline{n}$ = 1 of 12), 13% during 1990-91 ($\underline{n}$ = 1 of 8), and 0% during 1991-92 ($\underline{n}$ = 0 of 3). Wolves travelled 64 to 272 km (Table 5) to winter range; all movements occurred from October through February. Wolves

returned to their former territories during March through May.

The northernmost radio-marked wolf pack (Anisak Pack) occupied an area along the Noatak River (Fig. 5) in the vicinity of 2 wolf packs previously reported as migratory (Stephenson and James 1982). North of the Brooks Range we suspect that many of the packs may be migratory, following caribou to winter range. We reached this hypothesis because moose densities north of the Brooks Range are very low (i.e., <100/1,000 km^2). Low moose densities probably allows very few wolves to remain there on a year-long basis. Within the Brooks Range both resident moose and Dall sheep appear to be heavily preyed upon by wolves particularly during years of deep snow (J. R. Dau, Alas. Dep. Fish and Game, pers. commun.). In these areas sheep and moose numbers may be sufficient to support wolves on a year-round basis.

During 30-31 March 1989, we spent approximately 20 hours surveying wolves on caribou winter range in an area bounded by the Koyuk and Kiwalik Rivers on the west, Selawik River on the north, headwaters of the Huslia and Kateel Rivers on the east, and Shaktoolik River on the south. This was the first effort to determine wolf densities and distribution on caribou winter range since 1977 when wolf densities within the Selawik River drainage were estimated

at 12.9/1,000 km^2 (Davis and Valkenburg 1981). Snow and tracking conditions were sufficient to allow estimation of wolf numbers and distribution based upon track conditions, direction of movement, and pack size. This method has been widely used in Alaska for assessing wolf numbers (Stephenson 1978) despite its limitations and lack of precision (Ballard et al. 1993b).

During the survey we observed tracks of $\geq$ 5 wolf packs totaling 19 to 28 wolves. The wolf packs appeared to occupy discrete areas at the time of the survey and may have been territorial. These survey results, along with observed territory boundaries of radio-marked wolf packs suggest that most of the range of the WACH is occupied by territorial wolf packs. On caribou winter range, both territorial and migratory wolves exist but spatial relationships among these groups is unknown.

Dispersal

During our study, 21 wolves (13M, 8F) (25% of total) dispersed or left the territories in which they were originally radio-collared (Table 5). The sex ratio of dispersing wolves was not different from non-dispersing wolves (X^2 = 1.32, 1 = df, P = 0.25). Males dispersed an average distance of 154 $\pm$ 108.9 km whereas females dispersed an average distance of 123 $\pm$ 83.1 km; dispersal distances

were not significantly different (Z = -0.20, P = 0.84). Average age of dispersing males ($\bar{x}$ = 40.9 ± 33.9 months) was not significantly different from that of dispersing females ($\bar{x}$ = 35.0 ± 14.2); 31% of male and 43% of female dispersers were <24 months of age at time of dispersal. No radio-collared pups (≤12 months of age) dispersed during the study.

Because our frequency of relocations was not sufficient to determine exact dates of dispersal, we used median dates and the earliest dates that dispersal could have occurred (Fig. 6). Median dates represented the period of time from last known occurrence within the original territory to when wolves were first observed outside the original territory. Earliest dates of dispersal represented the period when wolves were last observed within their original territory. Wolves dispersed from their original territories during all months of the year. Both data sets suggested that dispersal in northwest Alaska was most prevalent from April through July (Fig. 6).

Status of dispersing wolves at time of last observation was variable (Table 5). Two dispersers pair-bonded with another wolf and formed a new pack, and 1 wolf joined an existing pack 375 km from its original territory. Seven wolves apparently continued to move away from the study area as radio contact was lost after dispersal had been

confirmed. Three apparent lone wolves were killed by hunters, and 5 were last observed alone. One wolf (No. 80) left its original territory accompanied by pups and was last observed 72 km from its original territory within the area previously or currently occupied by another pack (Dunes Pack).

Ballard et al. (1987) reported a dispersal rate of 28% in south-central Alaska; 40 to 50% were yearlings, and more males than females dispersed. Fuller (1989) reported that 35% of radio-collared wolves dispersed in Minnesota and there were no differences in dispersal rates by sex. Peterson et al. (1984) reported that annual dispersal rates for radio-collared wolves on the Kenai Peninsula, Alaska were as follows: 10% for pups, 17% for adults, and 49% for yearlings. Hayes et al. (1991) reported dispersal rates (29%) similar to those in south-central Alaska, but they found no difference between dispersal of males and females. Fates of dispersing wolves appear to be largely dependent upon the magnitude of human-caused mortality, density of prey, and the density of wolves within the area where they settle (Fritts and Mech 1981, Peterson et al. 1984, Messier 1985, Ballard et al. 1987, Fuller 1989).

Wolf dispersal rates in North America are determined by such factors as wolf and prey densities, pack sizes, territory sizes, and behavior (Packard and Mech 1980, Fuller

1989). Wolf densities and corresponding dispersal rates reported for North America were as follows: north-central Minnesota - 39-59 wolves/1,000 km^2, 35% (Fuller 1989); Kenai Peninsula, Alaska - 11-20 wolves/1,000 km^2, 33% (Peterson et al. 1984); north-western Minnesota - 10-30 wolves/1,000 km^2, 21% (Fritts and Mech 1981); southern Yukon Territory - 3.6-12.4 wolves/1,000 km^2, 29% (Hayes et al. 1991); south-central Alaska - 2.6-10.3 wolves/1,000 km^2, 28% (Ballard et al. 1987); and this study - 1.5-6.6 wolves/1,000 km^2, 25%. Peterson et al. (1984) suggested that, in relatively large packs, a higher level of social stress prompted more frequent extraterritorial movements. This speculation may also apply to dispersal rates. Dispersal rates are generally higher in relatively high density wolf populations. This density/dispersal relationship has implications for attempts to naturally restore wolf populations to areas where they have been extirpated. The relatively high dispersal rates for all wolf populations suggests that wolves are capable of colonizing new habitats if not subjected to high levels of human-caused mortality.

Wolves appear to disperse from original territories during all months of the year, but in arctic and subarctic areas peak dispersal occurs during late spring through summer (Peterson et al. 1984, Ballard et al. 1987, Hayes et

al. 1991, this study). Frequency of dispersals varies by geographic area.

A number of investigators have reported long distance dispersals by individual wolves (Van Camp and Gluckie 1979, Ballard et al. 1983, Fritts 1983, Hayes et al. 1991, Stephenson et al. 1993). Hayes et al. (1991) concluded that long distance movements of wolves between Canada and Alaska suggested that wolf distribution was dynamic and confirmed the phenotypic relatedness of the north-western gray wolf (Nowak 1983).

Wolf Density

We estimated autumn and spring wolf densities within the 12,279 km^2 study area using known numbers of wolves within radio-marked wolf packs. This procedure has been used elsewhere in North America (Fritts and Mech 1981, Peterson et al. 1984, Ballard et al. 1987, Fuller 1989, Hayes et al. 1991). We assumed that approximately 10% of the wolf population was composed of single wolves (Stephenson 1978, Ballard et al. 1987, Fuller and Snow 1988). However, this estimate may be too high because our radio-collared sample was composed of singles and pairs and consequently, perhaps no correction for single wolves was necessary. However, assuming 10% of the wolf population was composed of single wolves, spring wolf densities within the

study area increased from 2.7/1,000 km^2 in 1987 to 4.4/1,000 km^2 in 1990 (Table 6). Spring wolf densities declined to about 1.5 wolves/1,000 km^2 after 1990 because of a rabies epizootic and heavy human harvests.

The autumn wolf population increased at an annual finite rate of increase of 1.06 to 1.43 during 1987 through 1989 and then declined at an annual finite rate of about 0.64 (Table 6). Spring and autumn wolf populations exhibited similar trends. Extrapolation of wolf densities within the study area to all of northwest Alaska (119,140 km^2) suggested that during the study, wolf numbers varied from about 179 in spring 1991 (pre-denning) to 786 wolves in autumn 1989 (post-denning).

Habitat Use and Activity Patterns

There are few references in the literature concerning habitat use by wolves in North America. Although we had no estimates of habitat availability we did measure several parameters of habitats used by wolves (e.e., vegetation, slope, aspect, elevation). There were significant differences in use of slopes between summer and winter ($\underline{X}^2$ = 38.9, 7 df, $\underline{P} < 0.0001$). Wolves were observed using moderate slopes more frequently in winter than in summer and flat slopes more frequently in summer than winter, which contributed 87% of the Chi-square value (Fig. 7). There

were also significant differences in usage of aspects between summer and winter ($\underline{X}^2$ = 72.1, 21 df, $\underline{P}$ <0.0001) (Fig. 8). North-facing slopes were used significantly more during summer than winter and accounted for 43% of the Chi-square value.

Radio-marked wolf packs used spruce-dominated habitats on 55 and 58% of the relocations during summer and winter, respectively (Fig. 9). There were no differences in use of spruce habitats between summer and winter. There were significant differences in use of several other habitats between summer and winter ($\underline{X}^2$ = 122, 47 df, $\underline{P}$ < 0.0001). About 63% of the Chi-square value was due to differences in use of alpine herbaceous tundra, mat and cushion tundra, cottonwood (Populus balsamifera), marsh, and rock-snow habitats between summer and winter. Most of these habitats were used disproportionately more during summer than winter.

There were significant differences in activity patterns of wolves between summer and winter ($\underline{X}^2$ = 16.1, 9 df, $\underline{P}$ < 0.066) (Fig. 10). About 71% of the Chi-square value was due to differences between observed frequencies of feeding activity. Wolves were observed feeding proportionately more during winter than expected during summer. Fewer feeding observations during summer probably reflect lower observability of kill sites due to foliage and lack of snow. The relatively high number of observed kills during winter

probably reflects our intense daily tracking effort during periods of complete snow cover; few kills were missed and observability was high. Mech (1992) reported that during winter in northeastern Minnesota wolves exhibited the following percentages of activity: sleeping, 34%; resting, 31%; traveling, 28%; feeding, 6%; and other, 2%. Observed resting or sleeping activity in this study (i.e., 26%, Fig. 10) was considerably less than that observed by Mech (1992). We observed wolves running on 29 to 32% of the occasions they were observed. We suspect that our capture methods (use of fixed-wing aircraft and helicopter) contributed to fear of fixed-wing aircraft and caused some wolves to flee when aircraft were heard or seen. Also, wolves have been hunted legally and illegally from aircraft in this area. Statistical comparisons of our activity data to Mech's (1992) were not attempted because of biases introduced by wolves running in response to aircraft.

Wolves were found at relatively high elevations during January through May (Fig. 11) whereas lower elevations were used during December. Use of relatively high elevations during winter probably reflects selection of areas with lower snow depths. These areas are used also by caribou apparently because travel is easier where snow depths are lower.

Den and Rendezvous Site Use

We did not locate wolf packs frequently enough during late spring and summer to accurately document exact dates of den and rendezvous site usage. However, during daily relocation flights made for studies of predation rates we observed two packs returning to previously used dens as early as 5 and 9 April. On those occasions the wolves were observing digging snow out of the den. The earliest date that wolves were regularly observed attending a den site was 1 May. All denning wolf packs were regularly attending dens during May (n = 12). Based upon median dates of observation, wolf packs began attending den sites no later than the third week of May. These observations suggest that den use and parturition occur later than in south-central Alaska where packs were regularly using den sites by late April or early May (Ballard et al. 1987).

Re-use of den sites was documented for 4 packs that were relocated >2 years. One pack (Rabbit Mountain, relocated for 2 years) occupied different dens, while a pack monitored for 4 years occupied 1 site for 1 year and another site for 3 consecutive years. Two other packs (relocated for 5 years) used the same site each year. The pattern of repeated usage of the same den site is fairly common elsewhere in Alaska (Stephenson and Johnson 1973, Ballard

and Dau 1983) and in other areas in North America (Mech 1970).

Litter Size

Observed litter sizes ranged from 2 to 10 pups (Table 7). Although average annual litter sizes ranged from 3.5 to 6.4, they were not significantly different ($H = 8.17$, $P = 0.09$). Average litter size for all years pooled was 5.3 ± 2.0 ($n = 22$).

Our estimates of litter size underestimate actual productivity of this wolf population for several reasons. Pups do not come out of dens until they are 10 to 21 days old (Mech 1970, Clark 1971); consequently any mortality which occurred prior to, during, and after whelping would not be observed. Several of our observations were not obtained until late summer. Ballard et al. (1987) in south-central Alaska documented a decrease in average litter size from 5.5 to 5.3 between early and late summer. Similar losses were not measured in this study.

Fuller (1989) provided a summary of average litter sizes from 8 areas in North America. Lowest reported litter size was 4.4 from interior Alaska (Gasaway et al. 1982) whereas the largest litter size was 7.0 from northwest Minnesota (Fritts and Mech 1981, Harrington et al. 1983). Mean litter sizes from other areas were 4.9 for east-central

Ontario (Pimlott et al. 1969); 5.0 for the Kenai Peninsula, Alaska (Peterson et al. 1984); 5.6 for southern Quebec (Potvin 1988); 6.1 for south-central Alaska (Ballard et al. 1987); 6.4 for northeast Minnesota (Stenlund 1955); and 6.6 for north-central Minnesota (Fuller 1989). Our minimum estimate of 5.3 pups/litter is within the mid-range of reported wolf litter sizes.

Harrington et al. (1982) reported that frequency of multiple litters in wolf packs may range from 20 to 40%. Ballard et al. (1987) reported that multiple litters occurred in 7-10% of packs within a heavily exploited wolf population in south-central Alaska. No multiple litters were observed during this study. Van Ballenberghe (1983) suggested that conditions for occurrence of multiple litters included large territories with several potential den sites, adequate numbers of prey, and low human exploitation. Our study area met the first criteria but may not have met the last 2.

Boertje and Stephenson (1992) reported a relationship between wolf productivity and available ungulate biomass/wolf. With low ungulate availability (ungulate biomass indices/per wolf = 96-105), reproductively-active females averaged 4.6 fetuses per/female, while adult female wolves with relatively high prey availability (indices = 500-850) averaged 6.9 fetuses. Our reported minimum litter

size of 5.3 fell within the mid-range reported by Boertje and Stephenson (1992); at ungulate biomass indices of 180-390, adult females averaged 5.7 fetuses.

Territory sizes were large in northwest Alaska (see Territory Sizes and Movements), but numbers of available ungulate prey were variable during winter, and exploitation rates were relatively high (see Mortality). Fuller (1989) concluded that there was no relationship between average litter size and prey biomass per/wolf for 8 North American wolf populations. Explanation of the differences for frequency of production of multiple litters among wolf populations can not be explained at this time and warrants further investigation.

Survival.-- Because only 4 pups were radio-collared prior to April of each year (Table 1), we were unable to estimate pup survival rates. Estimates of yearling ($\geq$ 12 and < 24 months old) and adult ($\geq$ 24 months old) survival rates were obtained using Kaplan-Meier procedures (Tables 8-13). Overall, annual yearling female survival averaged 0.63 (Table 8). Survival rates in 1990-91 were significantly lower than those in 1987-88, 1988-89, and 1989-90 (Table 13). Yearling male survival rates which averaged 0.62 (Table 9) were not different (t = -0.18, 18.1 df, P = 0.86) from those of yearling females. When sample sizes were >1,

there were no significant differences in survival rates of yearling males among years (Table 9).

Adult females (≥ 2 years old) had an average annual survival rate of 0.66 (Table 10) whereas adult males averaged 0.59 (Table 11). Differences between adult males and females were not significantly different (t = 0.31, 71.6 df, P = 0.76). Annual survival of wolves differed among years (Table 13). Adult females had lower survival rates during 1989-90 and 1990-91 than during 1988-89. Survival rates of adult males were not significantly different among years (Table 13). However when the data were pooled by sex and age class there were significant differences in annual survival rates among years (Table 13). Most noticeable were the relatively low survival rates for 1990-91 (P values ranging from 0.016 to 0.176). We attributed the relatively low wolf survival rates during that year to high human harvests and the rabies epizootic which occurred that year.

For all wolves, annual survival rates averaged 0.59 (Table 12). Survival was greatest during summer months and began declining during winter due largely to harvest mortality. Weather conditions in northwest Alaska precluded hunting from snow machine during autumn and early winter due to inadequate snow cover and extreme winter temperatures. In February, snow depths were sufficient for snow machine travel and longer daylight hours and moderating temperatures

allowed local hunters to hunt for wolves. Fresh snowfall during these months allowed hunters to spot fresh wolf signs. Wolf hunting has been a traditional practice among Inupiat Eskimos. With the relatively recent acquisition of snow machines, wolf hunters have probably become more efficient (Alas. Dep. of Fish and Game, Div. Subsistence, Use of wolves by rural residents in GMUs 6 through 26: eight criteria worksheets, Alas. Board of Game, Juneau, 1989).

The overall annual survival rate of wolves (0.59) was slightly lower than that found in several areas of North America. Peterson et al. (1984) reported an annual rate of 0.67 on the Kenai Peninsula, Alaska and Fuller (1989) reported a rate of 0.64 for north-central Minnesota. Ballard et al. (1987) reported a rate of 0.48 for south-central Alaska and Hayes et al. (1991) reported a rate of 0.40 for the southern Yukon Territory. Values reported by Ballard et al. (1987) and Hayes et al. (1991) were considered to be indicative of heavily exploited wolf populations. Based upon this comparison, we judge the northwest Alaska population to have been moderately exploited. However, despite only moderate exploitation, survival was relatively low during 1990-91 (Table 13), and the wolf population declined. This decline was the result of a rabies epizootic. Also, our survival rate estimates may have been too high because pups were not radio-collared.

Pups often have lower survival rates than adults (Ballard et al. 1987, Hayes et al. 1991).

Peterson et al. (1984) and Messier (1985) reported that dispersing wolves suffered higher rates of mortality than resident wolves (e.g., 0.38 vs. 0.73 survival, respectively on the Kenai Peninsula). We compared overall annual survival rates by sex and age among dispersing and nondispersing wolves. There were no significant differences (P = 0.21-0.73) in survival rates between the dispersers and nondispersers for all wolves. Fuller (1989) in Minnesota and Hayes et al. (1991) in the southern Yukon Territory reported similar results.

Mortality

The causes of mortality of radio-collared wolves were classified as snow machine assisted hunting, aircraft assisted hunting, rabies, starvation, wolf predation, or old-age. Of the 85 wolves radio-collared, 28.3% were missing, had shed their collars, or were dead by April 1992 (Table 14). About 11% (n = 10) were alive when the study terminated: 2 were captured in 1989, 3 in 1990, and 5 in 1991. A minimum of 61% of the wolves died during the study period.

Hunting was the largest cause of death accounting for 69% of known mortalities (Table 14). Of that total, 4% were

taken by aircraft-assisted hunters and the remainder were taken by snow machine-assisted hunters. No radio-collared wolves were trapped. Natural causes accounted for 31% of the mortalities. The second largest cause of death was rabies (21%). Other causes of death included starvation (n = 3), wolf predation (n = 1), and old-age (n = 1).

Most (63%) mortalities occurred during December through March (Table 15). Of that total, hunting accounted for 89% of the mortalities. Rabies was a significant cause (21%) of mortality with 64% occurring during May and June. Although rabies is one of the oldest known diseases (Rausch 1973), this is the first study to document rabies as a significant source of mortality for a wolf population.

Rabies. Rabies has occurred sporadically in nearly all areas where wolves occur (Cowan 1949, Mech 1970, Rausch 1973, Tabel et al. 1974, Custer and Pence 1981, Sidorov et al. 1983, Bacon 1985, Butzeck 1987, and Zarnke and Ballard 1987). Mech (1970) suggested that rabies was 1 of the most important wolf diseases, but its role in limiting or regulating wolf populations was unknown. Only anecdotal accounts of mortality to individual wolves exist in the literature.

Rausch (1972, 1973) reported 5 cases of rabies among wolves during 1949 to 1972. The 3 known cases where humans have been infected occurred within or near our study area in

northwest Alaska (Rausch 1973, Ritter 1981). Chapman (1978) documented the occurrence of rabies within 1 wolf pack on the north slope of the Brooks Range during 1977. He observed 1 wolf, actively attacking other pack members at a rendezvous site. The attacking wolf was later diagnosed with rabies. At least 7 of 10 pack members were known to have died. Rabies was verified for 3 wolves, but cause of death of the others could not be verified because of decomposed carcasses. Alaskan wolves seldom die during summer (Peterson et al. 1984, Ballard et al. 1987). Therefore, rabies appeared to be the most likely cause of death for the other 4 wolves. At least 5 of the wolves died at 2 rendezvous sites. This fact caused Chapman (1978) to suggest that rabid wolves remained in familiar areas and were unlikely to transmit the disease to other wolf packs.

Davis et al. (1980) reported that wolf populations were relatively high in northwest Alaska during the early 1970 but declined after 1976. Rabies could have been one of several factors which caused the decline. However, this conclusion was conjectural since only 1 diagnosis was confirmed (Ritter 1981).

During 1989-1990, a rabies epizootic was confirmed in the wolf population in northwest Alaska (Table 14). During January and May, 3 radio-collared wolves from 2 packs were confirmed to have died from rabies. One of the wolves had

ingested porcupine (Erethizon dorsatum) quills. Rabid foxes frequently exhibit this behavior (Johnson and Beauregard 1969). During the ensuing 2 years, 11 wolves in 6 packs were thought to have died from rabies (Table 14). Ten of 11 deaths occurred during May through September. One winter mortality was confirmed. In the summer it was difficult to recover carcasses prior to the onset of decomposition. Only 3 wolves were confirmed rabid by laboratory examination. The remaining 7 wolves had decomposed to the point where laboratory examination was not possible. However, since there were no evident physical injuries in these wolves, we concluded that rabies was likely the cause of death. Ten of the 11 mortalities were females. Age structure of the mortalities was as follows assuming a 1 May birthdate for all wolves: 6 were 1-2 years old, 3 were 2-3 years old, 1 adult (>2 yr.) was unaged, and the single male was 4.3 years old. Total known or suspected mortality during 1989-1990 and 1990-1991 to the 6 packs was as follows: 5 of 21, 2 of 2, 1 of 7, 1 of 4, 1 of 2, and 1 of 1. These are minimum estimates of the extent of the epizootic because many wolves were not radio-collared. One uncollared wolf of unknown pack origin was killed in Ambler, Alaska (within Nuna Ck territory) and confirmed to have rabies (D. Ritter, State Public Health Lab., Fairbanks, pers. commun).

Blood samples were collected during tagging operations. Sera were tested for evidence of exposure to rabies virus by means of the rapid fluorescent focus inhibition test (Smith et al. 1973). Rabies is usually fatal to most mammalian species. Therefore, a low serum antibody prevalence would be expected. Only 2 of 83 sera (2.4%) tested during spring 1987 through 1991 had evidence of exposure to rabies virus: 1 of 7 in 1987, 1 of 10 in 1988, 0 of 23 in 1989, 0 of 28 in 1990, and 0 of 15 in 1991. Animals tested in 1990 and 1991 included wolves that ultimately died of rabies. Within Alaska, rabies virus is distributed almost exclusively along coastal regions in southwestern and northern portions of the State where red and arctic foxes are the primary hosts (Ritter 1981). However, the virus may occasionally occur in interior areas as well, although cases in either wild or domestic canids are rare (Ritter 1981). Zarnke and Ballard (1987) reported a low serum antibody prevalence for rabies in wolves from south-central Alaska during 1975-1982 (1 of 88, 1%).

The Nuna Creek pack was most affected by the rabies epizootic. The pack declined in numbers from 24 in autumn 1989 to 3 by autumn 1990. We do not know if reductions in pack size were due to rabies, dispersal, or illegal hunting but 5 rabies-caused mortalities were confirmed or suspected. A minimum of 5 pups were produced in 1990. They apparently

did not survive as only 3 wolves were present during autumn 1990. The 3 wolves survived the winter and entered the denning season. By autumn 1991, the pack numbered 19 suggesting that the rabies epizootic had ended. Possible explanation for the large increase in pack size include: pack size was under-estimated during winter 1990-1991, merging of other wolves into the pack, or production of 2 litters within the pack. Multiple litters in wolf packs have been previously reported (Harrington et al. 1982, Ballard et al. 1987). Rabies was present in fox populations during 1991 but apparently at lower levels, based on reported cases, than during 1989 and 1990 (Table 16).

Rabies outbreaks have occurred previously in northwest Alaska. Of the 3 known human deaths resulting from rabies, all have occurred in northwest Alaska; 2 were from wolf bites (Norvik and Wainright) and 1 from a dog (Candle)(D. Ritter, pers. commun).

During the same time period as our study, there apparently was also an epizootic in northeast Alaska (G. J. Weiler, United States Fish and Wildlife Service, Fairbanks, pres. commun.). Several wolves from different packs died and rabies could have been a significant mortality factor in that population.

Chapman (1978) observed that infected wolves remained in familiar areas. He hypothesized that they were unlikely

to spread the disease to other wolf packs. In our study, the packs known to have contacted rabies had territories that abutted ≥1 infected packs. Several avenues of contact were possible: infected wolves contacted other wolves along territory boundaries, infected wolves dispersed into other territories, or wolves contacted the virus from foxes. All known mortalities occurred within the known territorial boundaries of each pack. Distances from known den sites at the time of mortality ranged up to 22 km. Wolves in this area are generally not migratory. However, some packs may follow migratory caribou (see Territory Sizes and Movements) and some wolves disperse (see Dispersal). Contacts between rabid arctic and red foxes and wolves are probably most likely to spread the disease from pack to pack in northwest Alaska.

During 1971-1992, a total of 140 cases of rabies were confirmed in canid species in northwest Alaska (Table 16). These figures are minimum estimates because not all cases are reported or found. Arctic and red foxes accounted for 82% of the reported cases. During recent periods (1985-1992), an average of 18 cases/year were reported; 13 of 18 cases of rabies within dogs and wolves were also reported during this period. Foxes occurred within all wolf pack territories. We believe that foxes were the likely source of virus for introduction to the wolf population. Rabies

can eliminate entire wolf packs and can be a significant local limiting factor on wolf populations.

The 3 recent documented accounts of rabies in Alaskan wolf populations were discovered during short-term studies of wolf ecology using radio-telemetry. Without radio-telemetry, deaths from rabies would have gone unnoticed. Maintaining long-term contact with several wolf populations in different geographic areas may ultimately provide more evidence on the role of rabies in limiting or regulating wolf populations.

Hunting and Trapping. During 1985-86 through 1988-89, the wolf hunting season in northwest Alaska was 10 August through 30 April with no bag limit. Aircraft assisted hunting was allowed prior to the 1989-1990 season. Since the 1988-89 season the bag limit has been 10. Trapping seasons were 1 November through 15 April also with no bag limit. Trapping regulations allowed use of aircraft to locate wolves. Trappers were required to land and wait until the aircraft had stopped, and then exit the plane before firing. The procedure could be repeated as long as the aircraft did not harass the wolves. Beginning in 1988-1989, lands administered by the United States National Park Service were closed to the "land and shoot trapping method". This included Kobuk Valley National Park within the study area. Beginning in 1991-1992, this ban was extended to all

areas in northwest Alaska. Regulations required all hunters and trappers to present hides of harvested wolves to state officials for sealing. Data such as sex, color, and method and date of take were recorded on standard forms, and a seal was placed on each hide.

During 1985-86 through 1991-92, an average of 60 wolves were sealed annually within northwest Alaska (Table 17). Snow machine-assisted hunters and trappers accounted for 64% of the harvest while aircraft-assisted take accounted for 31%. After 1988-89 when "land and shoot" trapping was prohibited (excluding known illegal harvests), aircraft-assisted trapping composed only 8% of the reported harvests (Table 17); the latter animals were either trapped or snared with aircraft used for transportation to and from the area. Only 7% of all wolves killed during 1985-86 through 1991-92 were killed by steel traps or snares. Consequently, shooting from snow machine was the most common method of harvest.

Reported harvest dates indicated that most wolves (54%) were harvested during March and April (Table 18) when snow conditions aided locating and tracking wolves. Peak harvest dates were identical to those indicated by known dates of harvest for radio-collared wolves (Table 15).

Similar to captured radio-collared wolves, reported sex ratios within the harvest were significantly skewed towards

males ($\underline{X}^2$ = 18.4, 1 df, $\underline{P}$ < 0.00002) (Table 19). Although both harvest chronology and sex ratio data were similar to those provided by radio-collared wolves, total reported annual harvests are quite low in relation to actual harvests. Virtually all state annual survey-inventory reports have indicated that compliance with sealing requirements in northwest Alaska are low (Larsen and James 1987, 1988; Dau 1989a,b). These authors indicated that many wolves killed by northwest Alaska residents are used domestically and not sealed. They report that "local residents view many of the hunting and trapping regulations, and sealing requirements as excessively complicated and culturally inappropriate" (Abbott 1991:22).

Magnitude of the unreported harvest in northwest Alaska is unknown. Loon and Georgette (1989) reported that only 14-18% of actual harvests of grizzly bears by local residents were reported. Wolf population density within the study area was estimated for spring and autumn (Table 6), and these estimates compared to annual reported harvests (Table 17). These comparisons suggest that only 14 to 70% of the harvest may be reported annually. The estimates assumed that most losses from wolf packs during autumn through spring were related to hunting and trapping mortality. Compliance with sealing requirements appears to vary annually and differs among communities (Dau 1989a,b).

Because of noncompliance with sealing regulations, it is apparent that neither wolf population status nor total harvest can be accurately monitored with existing methods for collection of harvest data. Consequently, wildlife biologists must either develop wolf population census methods that provide at least an indication of population trend, or harvest reporting must be greatly improved. Simplification of caribou harvest reporting methods has not resulted in improved harvest reporting (Ballard et al. 1993a), which limits optimism for improved reporting for other species. Development of reliable wolf census procedures as described by Ballard et al. (1993b) appears to be the most promising method for assessing wolf population status.

Allowable Mortality Rates. We examined annual population dynamics of individual radio-marked wolf packs. We compared annual overwinter mortality caused primarily by humans (Table 15) with exponential rates of increase from spring to autumn for each pack using methods described by Ballard et al. (1987) and Fuller (1989). Percent overwinter mortality and annual exponential rates of increase (r) (Caughley 1978) were inversely correlated ($r = -0.60$, $P = 0.009$) (Fig. 12). On average each wolf pack would remain stable when mortality equaled about 53%.

Because harvest reporting compliance was low, we could not accurately determine the percent harvest from each pack as did Ballard et al. (1987) and Fuller (1989). Based upon known or suspected harvests and emigration and immigration rates within individual packs, we estimated that, on average, the wolf population might be able to sustain about 49% harvest mortality annually. The latter statistic should be used cautiously, however, because of the uncertainty of harvest rates. Also, the wolf population increased during the first 2 years of study but was declining the last 2 years (Table 6).

The relatively high incidence of rabies-caused mortality (i.e., 19% of population or 23% of all mortalities; Table 14) during the last 2 years of the study was a significant factor in causing the wolf population to decline. From October through April when pack numbers were estimated, $\geq$90% of the mortalities were due to humans followed by starvation, which accounted for 8% of the mortalities. Nearly all rabies-caused mortalities (91%) occurred during May through September. This source of mortality may have significantly reduced pup survival as it did for the Nuna Creek pack, but we have no evidence to support this suggestion because no pups were radio-collared. During years without rabies, total annual mortality >50% may

be sustainable depending upon sex and age structure of the population.

Based upon 9 studies in North America, Fuller (1989) indicated that wolf populations remained stable with overall mortality rates of 35% and human-caused mortality rates of 28% (Table 20). Contrary to the analyses based upon individual packs, our overall average rate of increase ($\underline{r}$ = -0.062; Table 6) in relation to estimated mortality rates of radio-collared yearling and adults (0.41, Table 12), suggests sustainable mortality rates in northwest Alaska are similar to the average values reported by Fuller (1989). One potential problem with estimating sustainable mortality rates based upon individual packs is that the sex and age structure of the pack can significantly affect the estimated rate of increase. Relatively small packs can sustain high mortality rates so long as reproductively active adults are not killed. Because wolf pups are more vulnerable to exploitation than adults, wolf populations composed of high proportions of pups can withstand heavier levels of exploitation than packs where adults compose a relatively high proportion of the harvest (Fuller 1989). Occurrence of multiple denning within individual packs (Harrington et al. 1982, Ballard et al. 1987) can also have a significant impact on rates of increase and sustainable mortality rates.

Feeding Ecology

During April 1987 through July 1992, we observed 19 radio-marked wolf packs at 184 prey carcasses; 90% were ungulates (Tables 21 and 22). Because all of the observations were made from fixed-wing aircraft, these values under-represent the importance of smaller prey such as snowshoe hares, muskrats (Ondatra zibethicus), and ground squirrels. Of the 184 observed carcasses, 4 (2%) were prey species other than ungulates, and 14 (8%) were unidentified.

Wolves killed 168 (91%) and scavenged 16 (9%) of the 184 observed carcasses (Tables 21 and 22). Caribou and moose composed 51% and 42% of the observed kills, respectively (Table 21). Adult (>2 yr) caribou (38%) and adult moose (25%) were the most frequently killed prey age class. They were also the most frequent age classes scavenged (Table 22). Moose calves composed the third (10%) most frequent prey type killed by wolves.

Moose and caribou were preyed upon by wolves during most months of the year. Months when these species were not represented in our data were due to seasonal distribution of caribou (see Caribou Distribution) and lack of detection of kills as a result of infrequent relocation of radio-marked wolf packs. Most (68%) ungulate kills were observed during March and April when we relocated several packs daily to document kill rates (see Kill Rates). Although we did not

conduct aerial surveys to ascertain sex-age composition of prey within all of the wolf study area, surveys in portions of the area allowed us to compare the age composition of wolf kills with those observed in the prey population.

Sex-age composition surveys of moose were conducted in the Tagagawik River moose count area (located just west of the study area) during autumns 1987 through 1989 and in 1992 (J. R. Dau, Alas. Dep. Fish and Game, pers. commun.). We used the sum of these counts to calculate expected calf:adult ratios. Because bears prey on moose calves during summer (Ballard 1992) and wolves most frequently prey on moose calves during winter (Peterson et al. 1984; Ballard et al. 1987; Gasaway et al. 1983, 1992), we reasoned most kills in winter could be attributed to wolves. If wolves were preying disproportionately on calves during winter when most of our observations occurred, then the percent calves of wolf-killed prey should differ from that within the prey population. Calf moose composed 16.7% of the moose observed during autumn counts (n = 1,487). We found no significant differences in age ratios of moose killed by wolves in comparison to calf:adult moose ratios for autumn (X^2 = 1.09, P = 0.30) counts. Wolves preyed on calf and adult moose in the same proportions that they occur within the moose population. This finding differs from that found elsewhere in Alaska and Canada.

Fuller and Keith (1980), Peterson et al. (1984), Gasaway et al. (1983), Ballard et al. (1987), and Hayes et al.(1991) indicated that wolves preyed disproportionately on calf moose during winter when deep snow made them particularly vulnerable. One major difference between the aforementioned studies and our study was that caribou were the primary prey species in this study, while moose were the primary prey in the others. One additional factor for consideration was the condition of moose killed by wolves.

Poor body condition of some moose may have made them more vulnerable to wolf predation. Based upon marrow fat values, we concluded that wolves were preying upon caribou that were in relatively good condition but moose that were in marginal condition (see Condition). If adult and calf moose were equally vulnerable or nearly so to wolf predation due to deep snow and marginal body condition, then perhaps wolves did not disproportionately select calves.

We also compared caribou age ratios between spring caribou counts conducted during 1987 through 1990 (Machida 1992) with calf:adult ratios of caribou killed by wolves. Wolves killed proportionately more adults and fewer calves (9-11 months-old) than expected based upon the spring counts ($\underline{X}^2 = 15.1$, $\underline{P} = 0.0001$). Wolves selected adult caribou and killed relatively few caribou calves during winter. Ballard et al. (1987) and Mech et al. (1993) also reported a

relatively low incidence of calf caribou being killed by wolves.

Distribution and Abundance of Caribou

Historically the WACH wintered on the Selawik National Wildlife Refuge and surrounding areas to the northwest, south, and east (Spindler 1989). The study area was selected by management biologists because at the beginning of the study it contained a wintering population of about 10,000 animals (D. James, Alas. Dep. Fish and Game, pers. commun.). However, during summer 1988, a wildfire burned over 84,580 ha within and adjacent to the study area. After the 1988 fire, most caribou wintered south of the burn in the Selawik and Nulato Hills (Spindler 1989, Machida 1992). Because of annual variation in use of the refuge as a caribou wintering area prior to the fire, it can not be assumed that the fire caused the caribou to winter elsewhere. However, for the short term the fire was likely a significant factor.

We monitored the occurrence of radio-collared caribou within the study area during January through April 1988-1990. The State of Alaska maintains $\geq$100 radio-collars within the herd to monitor general movement patterns and to assist with assessing general distribution during bi-annual photo-extrapolation surveys (Machida 1992). Although

portions of this herd migrated eastward from the calving grounds and rarely frequent the study area, we believed that the relative occurrence of radio-collared caribou within the study area provided an index of caribou abundance.

The percentage of radio-collared caribou occurring within the study area during January through April each year declined from 20.8% in 1988 to 5.7% in 1989 to 2.8% in 1990 (Table 23). Our incidental observations of numbers of caribou observed during radio tracking flights during these months followed this same trend. During April of each year, the percentage of radio-collared caribou that occurred within our study area increased several-fold. These changes reflect caribou migration to the calving grounds. However, even the relative proportions of migrating caribou during March and April declined each year. Consequently, available caribou for wolves declined as the study progressed.

During the study, caribou typically calved on the north slope of the Brooks Range during late May and early June. After calving, caribou began moving south and east and usually reached the Kobuk River between late August through October. They continued a southward movement and by late October and November about half of the herd was south of the Selawik Refuge (Machida 1992). Caribou used the wolf study area primarily during autumn and spring migrations. During these times from 1-32% of the WACH was present in the study

area depending on month and year (Spindler 1989). Caribou remained on the wintering grounds near the Nulato Hills, and large numbers of caribou occurred within the Shaktoolik, Ungalik, and Inglutalik river drainages (Machida 1992). Typical movement patterns of caribou are illustrated by movements of satellite-transmitter equipped caribou (Figs. 13-18).

Moose Abundance and Distribution

Moose colonized northwest Alaska during the 1940s and early 1950s (J. R. Dau, Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 1993). Moose populations increased in all areas through the mid- to late-1980s. Dau (1993) suggested that moose populations in at least some portions of northwest Alaska began declining about 1990. Reasons for the apparent decline are not known but severe winters and excessive predation have been proposed (J. R. Dau, Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 1993). Whether the moose population is exhibiting the classic eruption, decline, and stabilization phase suggested by Caughley (1970) is unknown. Dau (Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 1993) reported that 20%, 7%, and 2% of 45 radio-collared adult moose died within a 9-

month period in 1992 as a result of known or suspected predation, hunting mortality, and probable rutting-caused mortality, respectively.

Only 13% of cows with newborn calves (n = 54) had twins during 1986 in the lower Noatak River Basin (W. B. Ballard, unpubl. data). This twinning rate estimate was well below the average of 33% reported for 12 study areas in North America (Boer 1992). Relatively low productivity in combination with high mortality may have led to suspected moose population declines in northwest Alaska.

Distribution of moose within the study area has not been studied. However, our incidental observations during wolf and caribou radio-tracking flights suggest that distribution and habitat use patterns are similar to those reported by Ballard et al. (1987) in south-central Alaska. Moose typically use relatively high elevations during summer and autumn and move to lowland riparian areas for winter. We do not know if any moose within the study area are migratory, but if some are they probably follow major drainage systems to low lying areas. Moose densities within the Selawik National Wildlife Refuge that lies in the center of our study area were estimated by D. N. Larsen (Alas. Dep. Fish and Game, pers. commun.) at 166 moose/1,000 km^2 based upon a stratified sampling estimation procedure (Gasaway et al. 1986).

Kill Rates

During late winter and early spring 1988 through 1990, we intensively monitored 6 wolf packs on a daily basis to determine kill rates. We defined kill rate as the number of days/ungulate kill/wolf pack (Ballard et al. 1987). Because wolves prey on ungulates of various sizes, it can be misleading to report kill rates without adjusting for size of prey; kills of different sizes provide various amounts of flesh for consumption. We used the method described by Ballard et al. (1987) to adjust kill rates based upon sizes of prey. This procedure assigns values to each prey carcass equivalent to one adult moose (see Table 25 footnotes).

Fuller and Keith (1980) demonstrated that many studies have overestimated wolf kill rates based upon total number of observation days because wolves tend to remain on ungulate kills >1 day. Consequently the probability of finding wolves at a kill site with sporadic monitoring is greater than the actual kill rate. However, wolves can kill and consume some ungulates within a very short period of time. For example, during summer 1988, W. B. Ballard and D. N. Larsen observed a pack of 8 wolves kill, totally consume, and leave the kill site of a yearling caribou within 3 hours.

To reduce the potential bias reported by Fuller and Keith (1980), we eliminated the first survey day of each

sampling effort regardless of whether or not a kill may have been made. We relocated each wolf pack daily and attempted to track them in snow back to the previous day's location. This procedure allowed us to locate kills away from the pack. Tracking conditions were poor in 1988, and we must assume some kills were missed. For example, the Nuna Creek pack which had a traveling pack size of 4 (Messier 1985) (range = 1-9) was relocated on 28 consecutive days but no kills were observed. Tracking conditions within this area were poor and the pack frequently scattered and ran when approached by aircraft. Consequently, this pack was not used for calculation of kill or consumption rates. Tracking conditions were excellent in 1989 and 1990 and few kills should have been missed. However, a pair of wolves (Dunes pack) was relocated for 21 days in 1989 and no kills were observed. These wolves were also excluded from the kill and consumption rate analysis. We suspected the Dunes pack was scavenging kills and that we missed many of these carcasses. Such scavenged carcasses were old and covered with snow. Often there were no patterns to either wolf or prey tracks, nor were there signs of struggle at scavenged carcasses.

Between 11 March and 28 April during 1988 through 1990, we relocated 3 to 6 (total = 13) wolf packs (ranging in size from 1 to 23 individuals) each day (Table 24). Because pack members were not always located together due to dispersal or

fragmentation into subgroups for hunting, we used the average number of wolves observed during the study period for estimating kill rates. Messier (1985) and Dale et al. (1993) described this number as "traveling pack size". Thirteen packs were observed on 68 carcasses during the intensive study period. Seven (10.3%) were scavenged and not killed. These animals could have been killed by wolves prior to the intensive relocation effort. Each pack made an average of 5 ungulate kills (excludes scavenging) during the study period (Table 24).

Adult caribou (41%), adult moose (36%) and calf moose (13%) composed the observed kills (Table 24). Smaller packs (n = 3) composed of 1 to 4 individuals were responsible for all of the observed scavenging (7 carcasses). Numbers of ungulates killed/successful attack averaged 1.2 $\pm$ 0.83 (n = 54). Three cases of multiple kills were observed. The Dunes pack killed 2 adult moose on 13 April 1990, and the Purcell Mountain pack killed 7 adult caribou on 8 April 1990 and a cow and calf caribou on 14 April 1990. Other authors have reported multiple kills by wolves in other areas of Alaska (Eide and Ballard 1982, Dale et al. 1993). Dale et al. (1993) in Gates of the Arctic National Park reported a rate of 1.2 caribou/successful attack. Deep snow causes caribou to be vulnerable to wolf predation, and this factor was no doubt important in our study.

The 13 wolf packs were relocated an average of 18 ± 7.1 days (range = 6-28 days) (Table 25). Average pack size was 8.5 ± 6.6. We failed to relocate wolf packs an average of 1.2 ± 0.9 days per pack during the intensive study period (Table 25) due to inclement weather. Therefore, estimated kill rates should be viewed as minimal.

Each pack had an average of 809 ± 550 kg of killed prey available during the study (range = 81 for a single wolf to 1,694 for a pack of 13). Each pack killed an average of 1 ungulate/3.8 days unadjusted for prey size. Adjusted kill rates were somewhat lower (i.e., 1 kill [adult moose equivalent]/6.7 days).

We estimated the percent of each kill that had been consumed when first observed and attempted to document use of the carcass after the initial sighting. At first observation of a kill, an average of 53 ± 27% had been consumed (n = 75; note this number includes kills that were observed on the first day of monitoring which were deleted from kill rate estimates to avoid biasing the rates upwards). When each kill was last observed, consumption was estimated at 91 ± 15% (n = 53).

We also kept records of numbers of other scavengers attending kill sites, particularly ravens (*Corvus corax*). Hayes et al. (1991) indicated that in numerous wolf studies in North America (Peterson 1977, Fuller and Keith 1980,

Peterson et al. 1984, Messier and Crete 1985, Ballard et al. 1987) investigators have assumed that all available prey biomass (75% of prey weight) was available to wolves for consumption. Some investigators (Kolenosky 1972, Peterson 1977, Ballard et al. 1987) recognized that scavengers consumed portions of available prey but failed to estimate the amounts (Hayes et al. 1991). Promberger (cited as unpubl. data in Hayes et al. 1991) estimated that ravens consumed 10% of a carcass killed by a pack of 10 wolves, 20% from a carcass killed by a pack of 6, 50% from carcass killed by a pair, and 66% of a carcass fed on by a lone wolf. If these estimates are correct, our estimates of consumption should be adjusted accordingly.

The amount of a kill consumed by scavengers would depend in part on the numbers of ravens attending a particular kill site. The average number of ravens attending a kill site (with and without wolves) in this study was 3.7 $\pm$ 6.2 ($\underline{n}$ = 66; range = 0-30). Excluding 2 observations where 30 ravens were present caused the average number to decline to 2.7 $\pm$ 4.2. Based upon the low number of ravens attending kill sites, and the fact that each year there were a number of unretrieved hunter-killed caribou (W. B. Ballard, unpubl. data) we suggest that <10% of carcass biomass of wolf kills was consumed by ravens. Because this estimate was largely a guess, we chose not to modify

consumption rates as did Hayes et al. (1991). Despite our decisions, Hayes et al.'s (1991) point of considering scavenging activity in wolf consumption rates warrants further investigation.

Messier and Crete (1985) indicated that wolf kill and consumption rates were higher in areas with higher densities of moose. Fuller (1989) examined relationships between ungulate biomass indices and consumption rates among several North American wolf populations and found significant correlations between consumption rates and total ungulate biomass. We were unable to accurately calculate biomass indices for our wolf study area because of large seasonal and annual differences in caribou distribution. However, if we assumed minimum values of 166 moose/1,000 km^2 based on census data, and arbitrarily assumed a minimum of 2,000 caribou (i.e., 164/1,000 km^2) within the area on a year-round basis we derived a minimum biomass index of 267 (Table 26). We assumed that the captured wolves were representative of the wolf population and used their average weight (43 $\pm$ 5 kg, $\underline{n}$ = 90) for calculating consumption rates during the intensive study period. Each wolf had 5.3 kgs of ungulate prey per day or 0.17 kg/kg wolf/day (Table 25). Our estimates of wolf consumption rates and our admittedly crude biomass index were similar to Fuller's (1989)

conclusion that consumption rates increased with increasing ungulate densities.

We calculated the length of time that packs remained with kills (handling time) and the time interval that new kills were made according to species and sex-age class of prey. Because wolves can quickly consume caribou, we assumed that all kills of caribou and calf moose were made on the day of observation. For adult moose, however, if >50% of the carcass was consumed, we assumed the kill had been made after our last relocation the previous day. Length of time that wolves remained with carcasses appeared to be related to size of prey (Table 27). Wolves remained on adult female moose, adult bull moose, and adult male caribou carcasses an average of 2.0, 1.8, and 1.7 days, respectively. All other carcasses that involved single kills were attended by wolves for 1 day.

Messier and Crete (1985), Ballard et al. (1987), and Hayes et al. (1991) reported that smaller packs remained with adult moose kills longer than larger packs. We found no correlation between pack size and length of stay at adult moose kills (r_s = -0.37, P = 0.26), although singles and pairs appeared to fit this pattern. Ballard et al. (1987) and Fuller and Keith (1980) reported that wolves remained with adult moose kills for 2.7 and 2.5 days, respectively. Our reported interval was somewhat lower (1.8-2.0 days) than

those rates. Ballard et al. (1987) reported that wolves remained with adult caribou kills an average of 2.3 days, but rates in this study ranged from 1.1 to 1.7 days. Part of the discrepancy in these values may have resulted from the different method used by Ballard et al. (1987) to calculate occupation time. In that study, wolves were relocated every other day. The authors assumed that if any kill was consumed by >50% that it had been made the previous day. Because wolves can quickly consume small prey such as young caribou and moose, their estimates of occupation time may have been too high.

There was no consistent pattern between time interval between kills and size and number of prey killed (Table 28). Although larger packs appeared to have shorter kill intervals than smaller packs, pack size and time interval after kill were not significantly correlated for adult moose (r_2 = -0.51, P = 0.16) or adult caribou (r_2 = -0.32, P = 0.54). However, intervals after adult moose kills fit the pattern described by Ballard et al. (1987).

A relationship between wolf pack size and kill rates has been reported for several areas in North America; there is disagreement on whether the two variables are correlated (Peterson 1977, Messier and Crete 1985, Ballard et al. 1987, Sumanik 1987, Dale et al. 1993). Haber (1977) and Hayes et al. (1991) found no correlation between pack size and kill

rate, however Hayes et al. (1991) had a relatively large number of pairs and no large packs. We examined the relationships between pack size and adjusted kill rates and prey weight/wolf/day. Pack size and adjusted kill rates were negatively correlated (r_s = -0.59, P = 0.03), but pack size was not correlated with available prey weight/wolf/day with (r_s = -0.13, P = 0.67) or without scavenging (r_s = -0.08, P = 0.79). Because these types of analyses rely on a number of assumptions that may not be accurate, it is not surprising that there is considerable variation among studies.

We combined estimates from wolf-moose-caribou systems in Alaska and the Yukon (Ballard et al. 1987, Hayes et al. 1991, Dale et al. 1993, this study) to further explore these relationships. With this expanded data set wolf pack sizes and both adjusted kill rates (Fig. 19) and weight of available prey/wolf/day (Fig. 20) were significantly correlated (r_s = -0.64, P = 0.000007 and r_s = -0.29, P = 0.05, respectively). We conclude that pack size is a significant determinant of wolf kill rates but that considerable variation exists within and between study areas. Further, large sample sizes are probably necessary to accurately determine kill rates based upon pack sizes.

Wolves switched prey species as a result of changes in caribou distribution during the study (Tables 23 and 24).

During January through April 1988, when approximately 21% of the WACH radio collars were within the study area and caribou were abundant, 12 of 13 of the observed ungulate kills were caribou. During 1989 and 1990 when only 6 and 3% of the radio-collared caribou were within the area, respectively, caribou comprised 2 of 19 and 14 of 29 kills, respectively. If multiple kills of caribou were excluded from the 1990 estimate, only 5 of 20 of the 1990 kills were caribou. Our data suggest that wolves select caribou when available. Dale et al. (1993) concluded that wolves in Gates of the Arctic National Park killed caribou even when moose were twice as abundant as caribou. They saw no evidence of prey switching due to ungulate abundance. They suggested that moose within their area occurred at low densities and may have been in excellent condition, and consequently were relatively invulnerable to predation.

Burkholder (1959) suggested that wolves exhibited no selection for moose or caribou in south-central Alaska. Ballard et al. (1987) found that moose were the predominant prey but that wolves preyed upon caribou when they were available to resident wolf packs. Carbyn (1974) noted that mule deer (Odocoileus hemionus) were preferred prey in Jasper National Park, Canada, even though elk (Cervus elaphus) were more abundant. In Riding National Park (Carbyn 1983), elk were most heavily preyed upon, but white-

tailed deer (Odocoileus virginianus) were consumed disproportionately to available biomass. Dale et al. (1993) indicated that wolves continued to prey on caribou and did not switch to moose even when moose were numerically more abundant in Gates of the Arctic National Park, Alaska. In this study, wolves appeared to switch to moose when caribou were no longer available.

Dale et al. (1993) estimated that caribou and moose densities within individual wolf territories in Gates of the Arctic National Park, Alaska, averaged 227 ± 139 and 124 ± 43/1,000 km^2, respectively. The number of moose and caribou killed by wolves during March within individual territories averaged 13.4 (SD = 3.2) and 0.8 (SD = 1.2) per season, respectively. Although we did not determine prey densities within pack territories, we observed very few caribou in the study area during 1989 and 1990; caribou did not appear until late April when migration began. We only monitored signals of radio-collared caribou and did not specifically locate them; consequently, the presence of radio-collared caribou near the study area, did not mean they were within the pack territories we studied. We suspect that the major difference in our results and those of Dale et al.'s (1993) was that in our study wolf packs switched to moose, when caribou were largely nonexistent. We suggest there is a threshold density of caribou below the 200/1,000 km^2

reported by Dale et al. (1993) where wolves switch to more available prey.

During 1989 and 1990 when few caribou were present within the wolf study area, 3 of the packs moved from their territories to caribou winter ranges. This change from nonmigratory to migratory behavior was due to not enough preferred or alternate prey being available within the territory. Also during those years, ≥3 radio-collared wolves starved to death suggesting that prey abundance was low.

Age and Physical Condition of Ungulate Prey

Marrow fat of longbones has been widely used as an index of physical condition of ungulates at time of death (Cheatum 1949, Baker and Lueth 1966, Neiland 1970, Peterson 1977, Franzmann and Arneson 1976, Peterson et al. 1984, Ballard et al. 1987, Mech et al. 1993). For predator-killed ungulates, the hypothesis has been that ungulates with relatively high bone marrow fat values were not predisposed to predation while those with low fat values may have been predisposed. However, as pointed out by both Mech and Delgiudice (1985) and Ballard et al. (1987), statements about health of an animal near death are "one way"; it is easier to state with confidence that an animal had debilitating factors than to state it was completely

"healthy". Predator-killed animals seldom provide sufficient material for evaluation of body condition because many carcasses are fully consumed and only a few bone fragments remain (Ballard et al. 1981). Often the only remaining bones at a kill site are uneatable ramuses (Ballard et al. 1981).

Both Snider (1980) and Ballard et al. (1981) examined the relationships between mandible marrow fat and longbone marrow fat. There was a significant positive correlation between marrow fat levels in ramuses and other long bones. We combined the Ontario (Snider 1980) and Alaska (Ballard et al. 1981) data and developed a deterministic equation to estimate marrow fat in longbones based upon that found in ramuses. Davis et al. (1987) provided similar equations for caribou longbones (other than the femur) and ramuses. They found that evaluation of the amount of marrow fat in other bones besides femurs was useful for determining if an animal was in good or poor condition, but for comparative purposes it was useful to regress the values from other bones to the "femur standard". We regressed the marrow fat content in other bones to the femur standard and then compared our values with those reported in the literature.

During 1989 and 1990, we examined the nutritional condition of wolf-killed prey by using bone marrow fat levels. Ungulate carcasses killed by wolves ($\underline{n}$ = 22) were

examined *in situ* to determine species, age, sex, and physical condition of ungulates killed by wolves (Table 29). All examined ungulates were killed during the months of March and April, a period of time when marrow fat is near or at the lowest level of the year (Franzmann and Arneson 1976, Ballard et al. 1987). Twelve adult caribou (7F, 1M, and 4 unknown sex) and 10 yearling or adult moose carcasses (3F, 2M, 2 calves, 3 unknown sex or age) were examined. Average age of adult caribou and adult moose was 8.1 and 7.0 years, respectively. We combined carcasses of unknown sex with females, because sex ratios in the populations are weighted towards females (J. R. Dau, Alas. Dep. Fish and Game, unpubl. data).

Adult caribou killed by wolves during 1989 and 1990 had an average femur fat level of 79 $\pm$ 6% (n = 12) (Table 29). Marrow fat levels ranged from 13 to 96%, depending on type of bone examined. Adult female moose (n = 6) killed by wolves averaged 64% (range = 6-94%) femur fat. Two adult males and 2 calves of unknown sex averaged 29 and 55% femur fat, respectively. Average fat content by bone type for caribou and moose suggested that fat mobilization proceeded more quickly in proximal than in distal bones (Table 29). Peterson et al. (1982) and Davis et al. (1987) have previously reported this trend.

Franzmann and Arneson (1976) and Peterson et al. (1984) considered calf and adult moose with marrow fat levels of <10% and <20, respectively, to be near death from starvation. However, several authors have reported marrow fat levels >10% for calves that starved to death (Franzmann and Arneson 1976, Ballard et al. 1987). Fat levels for animals reportedly in good to excellent condition have ranged from 55% for red deer (Cervus elaphus)(Bubenik 1982), to 76% for pronghorn (Antilocapra americana) (Barret 1982), and 80% for elk (Greer 1968). Using the above criteria for moose and caribou, adult caribou killed by wolves had femur fat levels indicative of animals in good condition; only 1 caribou was near starvation (i.e., 26% fat). However, adult female moose and 2 adult males had relatively lower fat levels. Adult male moose were close to the 20% fat threshold starvation level.

Mech et al. (1993) suggested that use of <10% and <20% femur marrow fat as a threshold level for starvation was probably conservative, that these low levels ignored starvation physiology, and that using them could provide erroneous conclusions. They suggested that, when marrow fat levels were ≤70-87%, these levels should be thought of in terms of loss of body fat and muscle depletion. They believed that individuals with marrow fat levels ≤70-87% were in marginal condition.

We compared marrow fat levels for moose and caribou which died from starvation, wolf predation, and accidental causes from several areas in Alaska and the Yukon Territory (Table 30). Based upon marrow fat, Franzmann and Arneson (1976), Ballard et al. (1987), and Hayes et al. (1991) concluded that wolves were preying on adult moose that were in relatively good condition. However, Peterson et al. (1984) concluded that wolves preyed upon relatively old adults that had a high frequency of debilitating factors even though they were not malnourished. However, as pointed out earlier, low levels of bone marrow fat is only an indicator that an animal is definitely near starvation. It does not provide definitive data that an animal is necessarily healthy (Mech and Degiudice 1985, Ballard et al. 1987) and does not provide information concerning vulnerability. For example, deep snow in south-central Alaska during 1978-1979 exposed apparently healthy caribou to heavy levels of wolf predation (Eide and Ballard 1982). The comparison of our data with data from other studies, assuming that marrow fat is an indicator of condition, suggests that wolves preyed upon relatively healthy caribou and upon moose which were in marginal condition.

EFFECTS OF WOLF PREDATION ON WACH AND MOOSE

Most caribou calf mortality, as in many other North American ungulates (e.g., elk [Schlegel 1976], moose [Franzmann et al. 1980 and Ballard et al. 1981]), occurs during the first month of life (Whitten et al. 1992, Adams et al. 1993). Barren-ground caribou, unlike other ungulates, attempt to escape predators by calving on "calving grounds" that contain few alternate ungulate prey or predators (Bergerud and Page 1987, Fancy and Whitten 1991, Bergerud 1992). Although wolves can kill significant numbers of caribou on the calving grounds, much of the wolf-caused mortality occurs during migration and on wintering grounds. Bergerud and Ballard (1988, 1989) suggested that wolf predation could significantly limit calf recruitment when caribou fail to reach traditional calving grounds for parturition due to deep snow. In such cases, caribou are spaced out along migration routes where calves are subjected to predation by resident wolf packs. Such a scenario was postulated for the Nelchina caribou herd in south-central Alaska when calf recruitment was low during 1964-1966. Low recruitment coupled with heavy human harvests were thought to have initiated a population decline in that herd (Bergerud and Ballard 1988, 1989; Van Ballenberghe 1985, 1989). No attempt has been made to study caribou calf mortality on the calving grounds of the WACH. However, calf

survival has been sufficiently high to allow the herd to reach its current (1992) size of 417,000 from a low of about 75,000 (1976).

The total range of the WACH has been estimated at 362,600 km^2 (Davis et al. 1980). Extrapolation of average autumn wolf densities observed in this study (4.8/1,000 km^2) to the total range of the WACH yields a gross autumn wolf population estimate of 1,742 wolves. Although other areas within the WACH range apparently have higher densities (i.e., 7.4/1,000 km^2 in Gates of the Arctic National Park [Adams and Stephenson 1986] and 8.4/1,000 km^2 for Koyukuk National Wildlife Refuge [Spindler 1992]), from 33 to 50% of these wolves are killed annually. Using our estimated average prey weight available/wolf/day (5.3 kg) and assuming that 55% of the annual diet is composed of caribou, we estimated that wolves currently kill about 28,000 adult female caribou equivalents annually. This estimate suggests about 6-7% of the 1992 caribou population was killed by wolves. The WACH has been increasing at an annual rate of 11% since 1976 and wolf predation has not strongly limited caribou population growth. However, these data do not imply that wolf predation might not be a significant factor in the future.

When the WACH declined rapidly in the 1970s, excessive hunting and wolf predation were thought to be the cause

(Davis and Valkenburg 1985). Harvest reporting was virtually nonexistent at that time. Recently, concern has been expressed that the caribou herd may be approaching ecological (habitat) carrying capacity (Machida 1992). Caribou populations that are not subject to hunting or predation become regulated by food competition at densities >2,000/1000 km^2 (Bergerud 1983, Skogland 1985). Current WACH densities are about 1,149/1,000 km^2, with wolf densities ranging from 4.8 to 8.4/1,000 km^2 (Spindler 1992, Dale et al. 1993, this study). Unfortunately, caribou harvest reporting is still poor (Machida 1992). Caribou recruitment may begin to decline in response to declining habitat quality and large (unreported) harvests. If the population declines as drastically as it did during the 1970s, wolf predation could become a significant source of mortality. Continuation of bi-annual censuses should alert managers when a decline is in progress. Reductions in human harvest would also help to reverse a declining trend (Davis and Valkenburg 1985).

Wolf populations in northwest Alaska are limited by hunting and trapping. Based upon Fuller's (1989:21) relationship between ungulate biomass and wolf densities for several areas in North America, the predicted wolf density for northwest Alaska would be about 16.4 wolves/1,000 km^2 (assumed 1,149 caribou/1,000 km^2 and 200 moose/1,000 km^2).

Bergerud and Elliot (1986) predicted that caribou population growth would halt in systems where caribou were the principal prey and wolf densities attained about 6.5/1,000 km^2. Because northwest Alaska has moderate to low moose densities, wolf densities could probably be higher than 6.5/1,000 km^2 before caribou population growth would halt. Wolf densities in our study area only reached the level suggested by Bergerud and Elliot (1986) in autumn 1989 and have since declined. However, other areas within the WACH range have higher wolf densities. Also, inclusion of large areas into the National Park System has reduced hunter access; harvests are now low, and wolf densities may have increased in those areas (J. R. Dau, Alas. Dep. Fish and Game, pers. commun.).

Biologists have expressed concerns over the widely fluctuating densities of caribou that have historically occurred in northern Alaska and elsewhere. Managers have attempted to slow herd growth rates by liberalizing caribou hunting seasons and bag limits. If managers wish to slow herd growth rates and attempt to stabilize the WACH, they might consider allowing wolf populations to increase beyond current levels earlier in the caribou growth phase. A larger wolf population would slow or halt caribou population growth. However, under the current harvest regime, we doubt that wolf populations in our study area can achieve higher

densities than those observed. Therefore, if managers wish to halt caribou population growth, initiation of wolf conservation measures within northwest Alaska will probably be necessary. However, allowing wolf densities to increase could also increase predation on resident moose populations.

Effects of Wolf Predation on Moose

Prior to initiation of this study, historical reports and conventional wisdom suggested that a large portion of the wolf population within the WACH was migratory. This conclusion was based upon studies in Canada (Kuyt 1972, Parker 1972) and Alaska where limited movement data and historical reports from biologists and local users (Hakala 1954, Kelly 1954, Stephenson and Johnson 1973, Stephenson and James 1982) suggested that wolves followed caribou to wintering areas. Our study, and those of Spindler (1992) and Dale et al. (1993) suggest that wolves within the range of the WACH are largely territorial and generally do not follow caribou to wintering grounds; the few packs that do follow migratory caribou, apparently do so initiated in response to a lack of prey within the territory. Such movements do not occur annually and are not predictable from year-to-year unless prey numbers are known.

Prior to the 1940s, there were few, if any, moose within northwest Alaska (J. R. Dau, Noatak River moose radio

telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue; 1993). Dau indicated that during the late 1940s and early 1950s moose colonized northwest Alaska. The moose population grew through the mid- to late 1980s. If historical wolf densities were substantially greater than current densities, wolf predation may have been an important factor in preventing earlier colonization by moose. After 1990, Dau felt that a "widespread" decline had begun in the moose population in at least portions of the Seward Peninsula and Kotzebue Basin.

We speculate that the recent occurrence of moose in northwest Alaska has altered the historical migratory patterns of wolves. Prior to colonization by moose, caribou were the principal prey species of wolves. Although Dall sheep occur within the Brooks Range, their importance as wolf prey is unknown. Several studies in other areas suggest that wolf predation on sheep is relatively low (Sumanik 1987, Barichello et al. 1989b) and they are not important to wolves. However, Murie (1944) suggested that wolf predation limited lamb recruitment when caribou were unavailable to wolves. In addition, recent incidental observations of wolves preying on sheep in the Baird and Delong Mountains suggest that wolf predation may be an important cause of sheep mortality during some years (J. R. Dau and L. A. Ayres, Alas. Dep. Fish and Game, pers.

commun.). Dau and Ayres have suggested that these areas have less sheep escape habitat than many other areas in Alaska, and consequently sheep are more vulnerable to wolf predation during years of deep snow. If this suggestion is correct, resident sheep populations and the recent occurrence of moose in the area may provide sufficient alternate prey so that wolves no longer have to migrate. If our hypothesis is correct it has ramifications for both wolf and ungulate management objectives.

Resident wolf packs in northwest Alaska clearly select caribou as prey when they are available. When caribou migrate and are virtually nonexistent, wolves switch to moose or possibly sheep as the principal prey, or they migrate if sufficient alternate prey are not available. Bergerud (1974), Bergerud and Elliot (1986), and Seip (1992) believed that woodland caribou (R. t. caribou) declines in British Columbia were the result of colonization by moose followed by increased wolf numbers and consequently increased predation on caribou. Seip (1992:1500) stated "... wolves were sustained primarily by moose throughout the year, but became a major predator on caribou during summer, when caribou, wolves, and moose occupied similar areas and habitats." We suggest the possibility that the reverse could be true in northwest Alaska.

There is some evidence to support our speculation that wolf packs became less migratory and a resident territorial system developed when enough prey was available in areas to sustain wolves on an annual basis. Bergerud and Manuel (1969), Messier and Crete (1985), and Gasaway et al. (1992) indicated that moose occur at densities <400/1,000 km^2 when wolves are present and uncontrolled. When predator densities are greatly reduced, moose attain densities of 2,000 to 4,000/1,000 km^2. In our study area wolves primarily select caribou as prey, but when caribou are not available, predation shifts to moose. Relatively high caribou populations may allow wolf densities to increase based upon the caribou prey base. However, when caribou leave, relatively high wolf densities may put disproportionate predation pressures on moose and possibly sheep.

We estimated the potential impact of wolf predation on resident moose populations by assuming that wolves switched to moose when caribou were absent for 4 months each year. We used the highest observed autumn wolf density and the average for the study. We assumed that, during the 4 months that caribou were absent, moose composed 78% of the diet (Table 24: 1989 data and multiple kills of caribou were excluded). During the remainder of the year moose composed 46% (Table 21) of the wolf prey. We assumed that winter and

summer wolf kill rates were similar (James 1983, Ballard et al. 1987). Moose densities for the study area were assumed to be 166/1,000 km^2 (D. N. Larsen, pers. commun.). Assuming a wolf consumption rate of 5.3 kg/wolf/day, wolves would kill from 216 to 295 moose (Ad F moose equivalents)/year or from 11 to 14% of the moose population annually. In some areas sheep may also experience relatively high rates of mortality due to wolf predation. These estimates of mortality due to wolves combined with unreported human harvests and severe winter conditions could cause moose and sheep densities to decline dramatically in northwest Alaska. Dau (Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 1993) recently reported that 20 of 45 adult moose radio-collared in the Noatak River drainage during April 1992 died during 1992-1993 and that 9 (20%) died as a result of known or probable predation.

Brown and black bears have been identified as important predators of moose in North America (Franzmann et al. 1980, Ballard et al. 1981, Ballard and Larsen 1987, and Ballard 1992). Bear predation on either moose or caribou has not been studied in northwest Alaska. However, over a 5-year period Ballard et al. (1993a) observed 30 radio-collared bears feeding on 38 ungulate carcasses (i.e., 17 moose, 9 caribou, and 12 unidentified) in the Noatak River area of

northwest Alaska. Ballard et al. (1993a) also observed bears actively killing newborn moose calves. Brown bears have been reported to kill from 6 to 52% of newborn moose calves in some moose populations and are an important predator on adult moose as well (Ballard 1992). Combined bear and wolf predation, particularly when caribou are not available, could be the cause of the apparent moose decline reported by Dau (Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 1993) in several portions of northwest Alaska. Our analyses suggest that although the WACH would not be negatively affected by allowing wolf densities to increase, resident moose populations could be significantly impacted during years that caribou are unavailable to wolves as winter prey.

CONCLUSIONS

1. Sex ratios of pups favored females and yearling sex ratios were equal. Adult sex ratios favored males possibly due to observer selection. Reasons for differences in sex ratios among North American wolf populations are unknown.

2. Six wolf packs were relocated frequently enough to estimate seasonal and total territory size. Winter territories ($\bar{x}$ = 2,474 km^2) were significantly (P = 0.03) larger than summer territories ($\bar{x}$ = 1,251 km^2). Year-round territories averaged 3,652 km^2. Territory sizes were significantly correlated with pack size (P = 0.007). Although historical reports indicated that wolves in northwestern Alaska followed migratory caribou, we found that most wolf packs were sedentary and maintained annual territories. Some wolf packs (n = 4) occasionally followed migratory caribou from 64 to 272 km when caribou and moose densities (i.e., <100/1,000 km^2) were relatively low within an individual territory. Wolf migration was not predictable. We postulate that relatively recent colonization by moose has altered wolf movement patterns. Moose densities in many areas (>150/1,000 km^2) may be sufficient to sustain wolf populations when caribou are absent and consequently migration is no longer necessary. Although some wolf packs within the range of the Western

Arctic Caribou Herd are probably migratory, available data suggest that most maintain annual territories.

3. Twenty-five percent of the radio-collared wolves dispersed during the study. This magnitude of dispersal appears typical of many North American wolf populations that depend primarily on moose and caribou as prey. There was no difference in sex ratios between dispersing and non-dispersing wolves. Males dispersed an average distance of 154 km and females 123 km, but the distances were not statistically different. Most dispersal in northwest Alaska occurred during April through July. Fates of dispersing wolves were largely dependent on the magnitude of human-caused mortality. There were no differences in survival rates between dispersing and non-dispersing wolves.

4. In relation to available ungulate biomass, wolf densities within northwest Alaska were relatively low (1.5 to 6.6 wolves/1,000 km^2). Based upon the relationship of available ungulate biomass to wolf densities elsewhere in North America, predicted wolf densities were 16.4/1,000 km^2. Annual finite rates of increase ranged from 0.64 to 1.43 during the study (spring rates averaged 0.97). Wolf densities increased during 1987 through spring 1990 and then declined in response to a combination of human harvest and rabies.

5. We found significant differences in use of slopes, aspects, and habitats by wolves between summer and winter. Wolves used flat slopes more in summer than winter and moderate slopes more in winter than in summer. North-facing slopes were used more during summer than winter. Wolves were located most frequently in spruce dominated habitats. Wolves used alpine herbaceous tundra, mat and cushion tundra, cottonwood, marsh and rock-snow habitats more in summer than during winter. Activity patterns were similar to those observed in northeast Minnesota except that we observed a relatively high proportion of running behavior. We attributed this behavior to wolves being alarmed by aircraft. Use of aircraft in capture operations and hunting activities may have accounted for this behavior. Wolves were observed in more feeding activity during winter than during summer. Dense foliage during summer probably caused us to underestimate the number of kills made by wolves, while the relatively high incidence of feeding activity during winter was probably the result of complete snow cover and frequent relocation of radio-collared wolves.

6. Wolves were first observed visiting den sites during April. Denning packs were regularly attending den sites by mid-May. Den use and parturition probably occurred slightly later in more southern latitudes. Den use appeared to be fairly traditional. Minimum estimates of litter size

averaged 5.3 and was comparable to estimates for other wolf populations with moderate to high prey availability.

7. Annual survival rates for yearling females and males each averaged 0.63. There was no significant difference ($P = 0.76$) between average annual survival rates of adult females (0.66) and males (0.59). Overall, there were differences ($P < 0.05$) in average survival rates among years. The low survival rate of 1990-91 was attributed to a combination of high human harvests and a rabies epidemic.

8. Most (61%) of the wolves radio-collared during this study died. Twenty-six percent were missing when the study was terminated in 1992. Hunting accounted for 69% of the known mortalities. Natural mortality accounted for 31% of the mortalities with rabies being the second largest cause of death (21%). Sixty-three percent of the mortalities occurred during December through March, and hunting accounted for 89% of the mortalities. Sixty-four percent of the rabies-caused mortalities occurred during May and June. This study was the first to document that rabies can be a significant limiting factor of wolf populations. Other studies have only reported individual accounts of rabies, usually restricted to single packs. Patterns of annual harvest according to harvest records were quite similar to that observed based upon radio-collared wolves. The numbers of wolves annually killed in northwest Alaska by local

hunters and trappers is largely unknown because of poor compliance with state sealing regulations. The wolf population appeared to sustain about 30 to 40% hunting mortality annually.

9. Nineteen wolf packs were observed on 184 carcasses: 168 killed by wolves and 16 scavenged. Caribou and moose composed 51 and 42% of the kills, respectively. Adult caribou (38%) and moose (25%) were the most frequently killed age classes. Most (68%) of the ungulate kills were observed during winter during March and April when several packs were relocated daily. Wolves appeared to prey on calf and adult moose in proportion to their occurrence in the moose population while adult caribou were killed disproportionately. Wolves did not select caribou calves.

10. Several wolf packs were relocated daily during March and April 1988 through 1990 to determine species composition of prey and kill rates. We determined caribou abundance within the study area by monitoring the numbers of radio-collared WACH within the area. Caribou were relatively abundant within the study area during 1988 and relatively scarce during 1989 and 1990. Moose colonized the study area during the 1940s and 1950s and attained densities of about 166/1,000 km^2. Thirteen wolf packs were observed on 68 carcasses of which 7 were scavenged. Small packs of 1-4 individuals were responsible for all observed scavenging.

Adult moose and caribou composed 41 and 36% of the observed kills. Calf moose were the third most common prey. Several instances of multiple kills of caribou were observed. Numbers of ungulates killed/successful wolf attack averaged 1.2 ($\underline{n}$ = 54). Kill rates were adjusted to an adult moose equivalent and averaged 1 kill/6.7 days. Carcass consumption at first observation averaged 53 and 91% at last observation. Scavenging, particularly by ravens, influenced wolf consumption rates but we were unable to estimate its magnitude. Each wolf had 5.3 kg of ungulate prey available/day or 0.17 kg/kg wolf/day. Other North American studies indicated that wolf consumption rates increased with increasing prey densities. Wolves remained with adult female moose, adult bull moose, and adult male caribou an average of 2.0, 1.8, and 1.7 days, respectively. We found no correlation between pack size and length of time that wolves remained with kills. There was no consistent pattern between time interval between kills and size and number of prey killed species. Pack size and time interval between kills was not correlated. Pack size and adjusted kill rates were negatively correlated ($\underline{P}$ = 0.03), but pack size and available prey weight/wolf/day were not ($\underline{P}$ = 0.67). Comparisons between pack size and kill rates reported among several studies in North America where caribou and moose were the principal prey species showed significant

correlations between pack size and kill rates, and pack size and available prey/wolf/day. However, there is considerable variation within and among studies and pack size is probably not a reliable indicator of kill rate.

11. Wolves preyed primarily on caribou when they were available. When caribou migrated and caribou densities were low (<200/1,000 km^2) wolves switched to moose. Adult caribou killed by wolves had average femur marrow fat levels averaging 79% while female marrow fat levels in adult moose averaged 64%. Ungulates with marrow fat levels $\leq$70-87% were probably in marginal condition. We concluded that wolves preyed on caribou that were in relatively good condition but that adult moose prey were in marginal condition.

12. Based upon estimated wolf densities within the range of the WACH, estimated kill rates determined during this study, and available ungulate population estimates, we estimated numbers of caribou and moose that were being killed annually by wolves in northwest Alaska. We estimated that wolves kill from 6 to 7% of the caribou and from 11 to 14% of the moose population annually. Based upon ungulate biomass indices alone, northwest Alaska should be able to support about 16 wolves/1,000 km^2. However, due to territoriality, wolves switch to preying on moose and possibly sheep when caribou leave the area. The estimated kill rates of moose by wolves and (unreported) humans may be sufficient to cause

a significant decline in the moose population. Wolf densities could be higher in northwest Alaska if maintenance of current moose population density were not a management priority.

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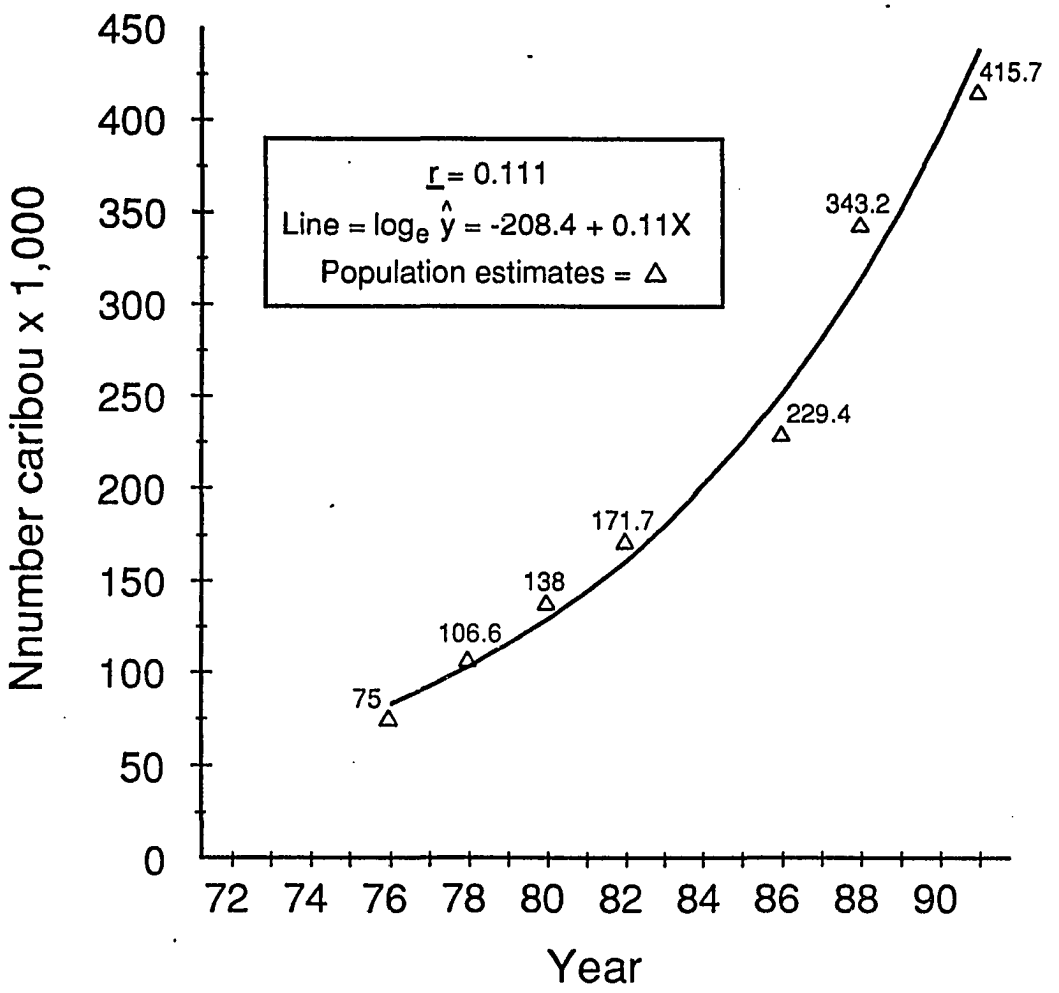


Fig. 1. Projected population growth of the Western Arctic Caribou Herd based upon population estimates obtained during 1976 through 1992. Population estimates obtained from Davis and Valkenburg (1978), Machida (1992), and J. R. Dau (Alas. Dep. Fish and Game, unpubl. datapers. commun.).

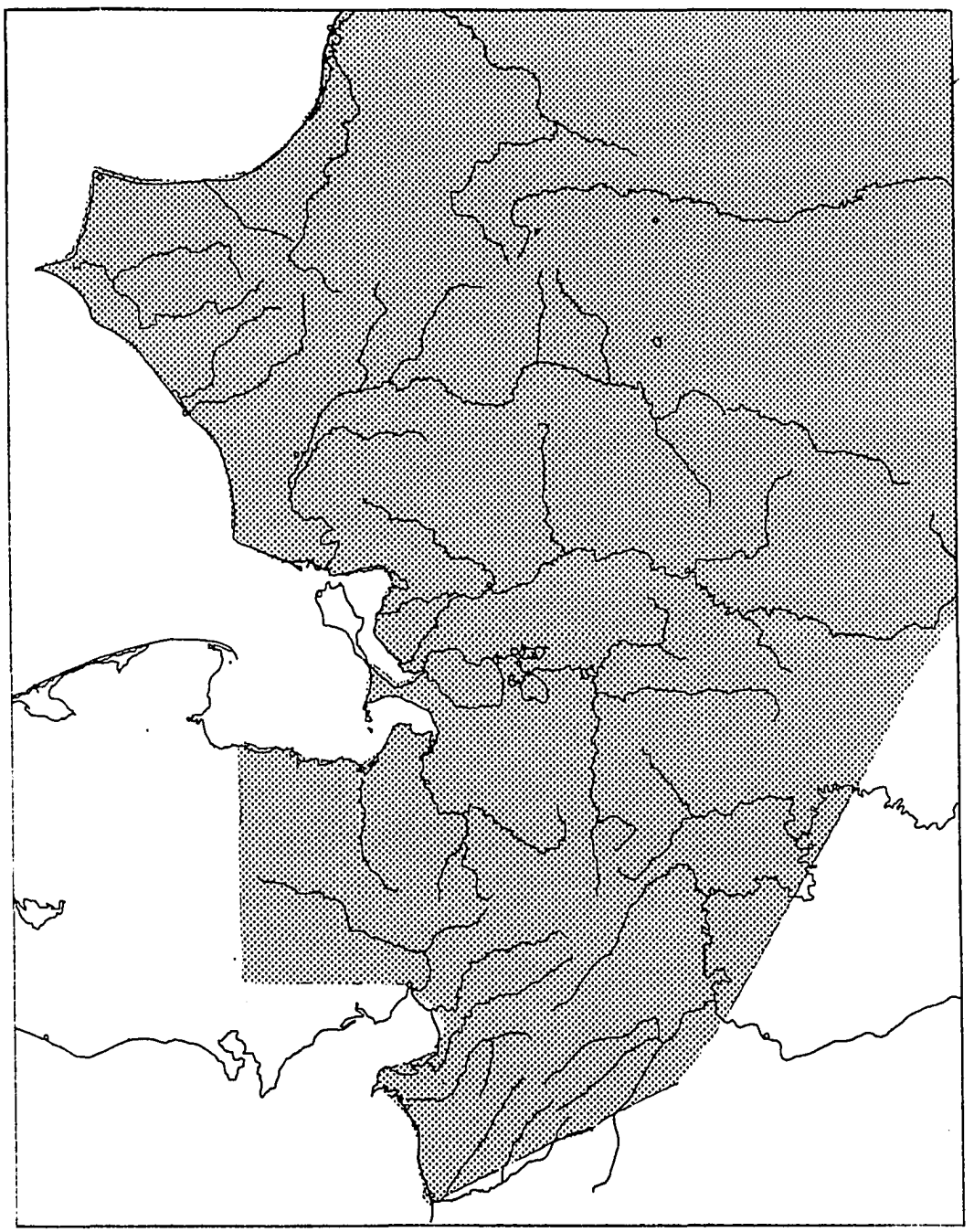


Fig. 2. Distribution of the Western Arctic Caribou Herd during the late 1970s through the early 1980s in northwest Alaska as determined from radio telemetry (from Davis et al. 1980).

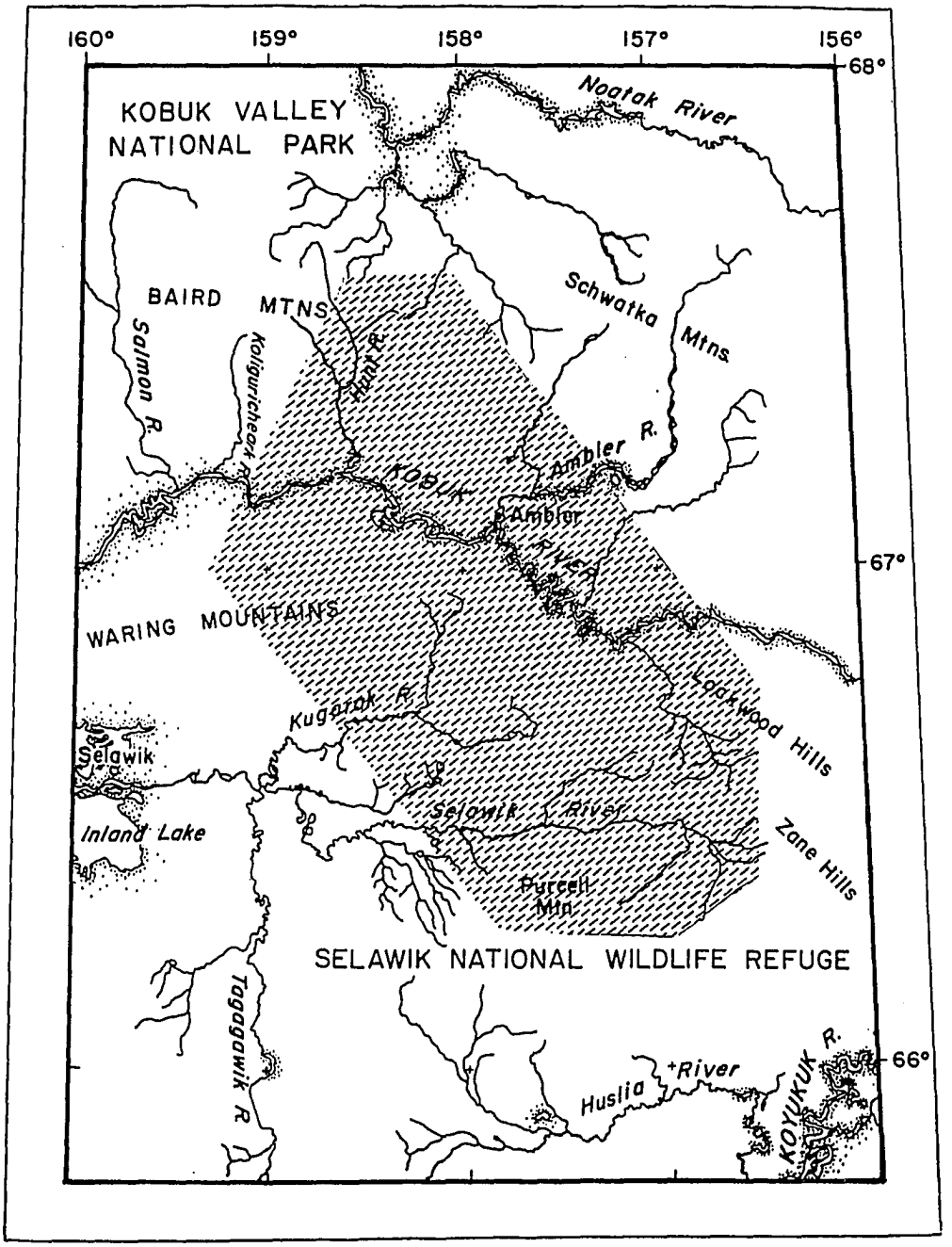


Fig. 3. Approximate boundaries of wolf study area in northwest Alaska, April 1987 through July 1992.

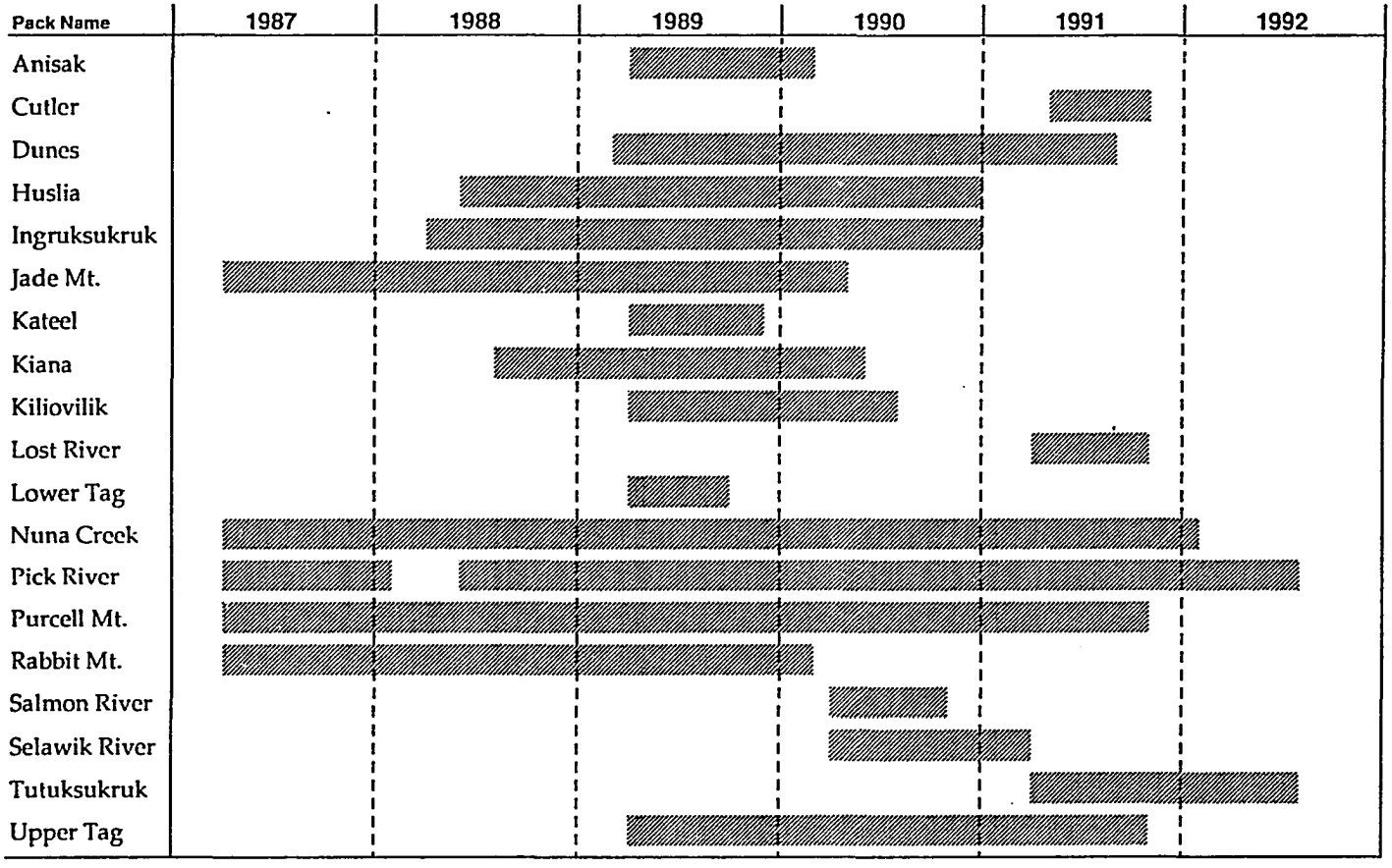
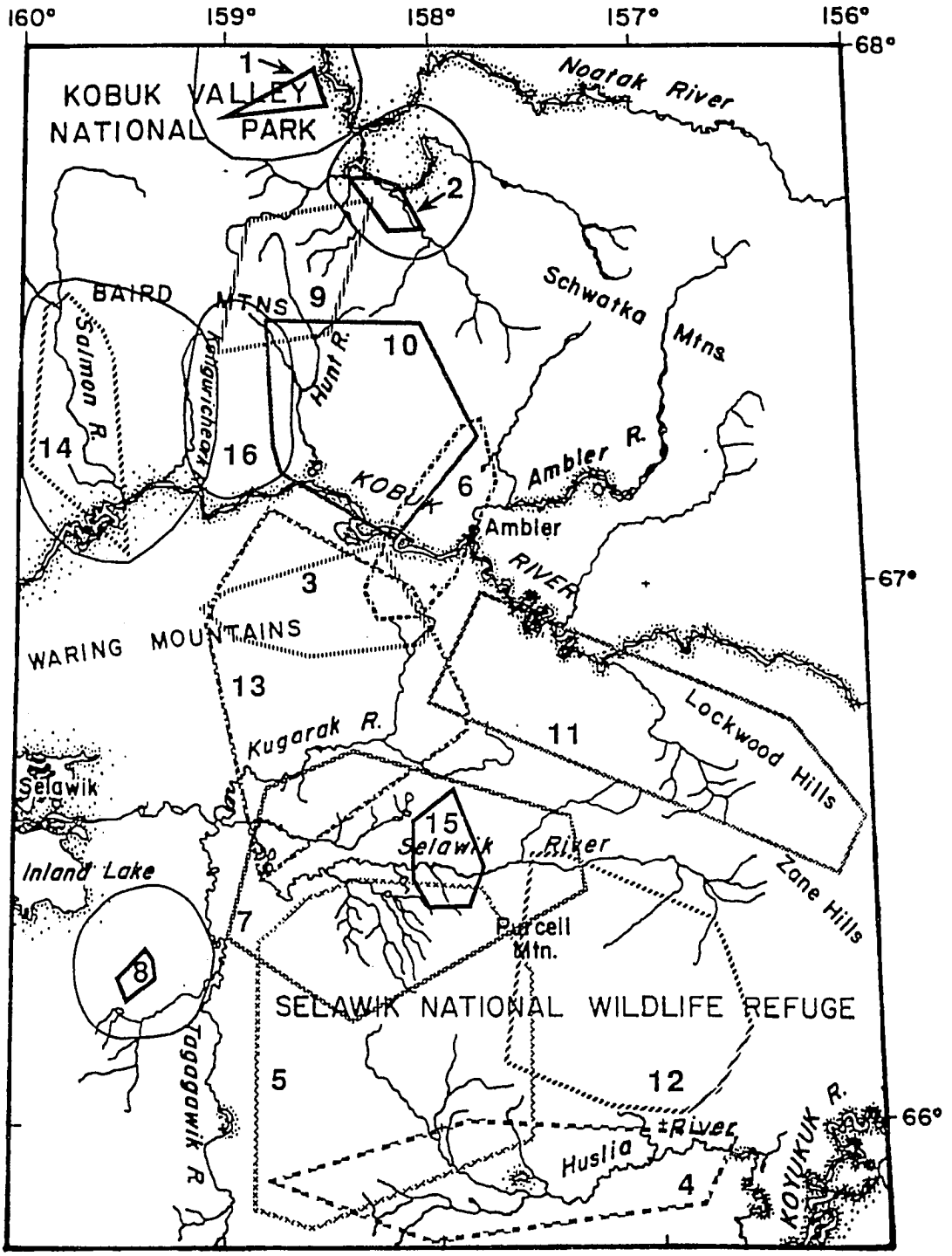


Fig. 4. History of radio contact with individual wolf packs which were studied in northwest Alaska, April 1987 through July 1992. Solid line indicates periods of continuous radio contact.

Fig. 5. Observed territory boundaries (convex polygons) of 16 wolf packs that were studied in northwest Alaska, April 1987 through July 1992. Territory boundaries represent minimum areas for ≥9 packs (3 packs not shown) that were located too infrequently to accurately determine territory size. Dotted lines are estimated territory boundaries. Numbers correspond to the following packs: 1 = Anisak, 2 = Cutler River, 3 = Dunes, 4 = Huslia, 5 = Ingruksukruk, 6 = Jade Mountain, 7 = Kiliovilik, 8 = Lower Tag, 9 = Lost River, 10 = Nuna Creek, 11 = Pick River, 12 = Purcell Mountain, 13 = Rabbit Mountain, 14 = Salmon River, 15 = Selawik River, and 16 = Tutuksuk.


160°
159°
158°
157°
156°
68°
67°
66°
KOBUK VALLEY NATIONAL PARK
Noatak River
BAIRD MTNS
Salmon R.
Kelgurichpak
Hunt R.
Schwatka Mtns
Ambler R.
KOBUK
Ambler
RIVER
WARING MOUNTAINS
Kugarak R.
Lockwood Hills
Selawik
Inland Lake
Selawik River
Zane Hills
Purcell Mtn.
SELAWIK NATIONAL WILDLIFE REFUGE
Togagawik R.
Huslia River
KOYUKUK R.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

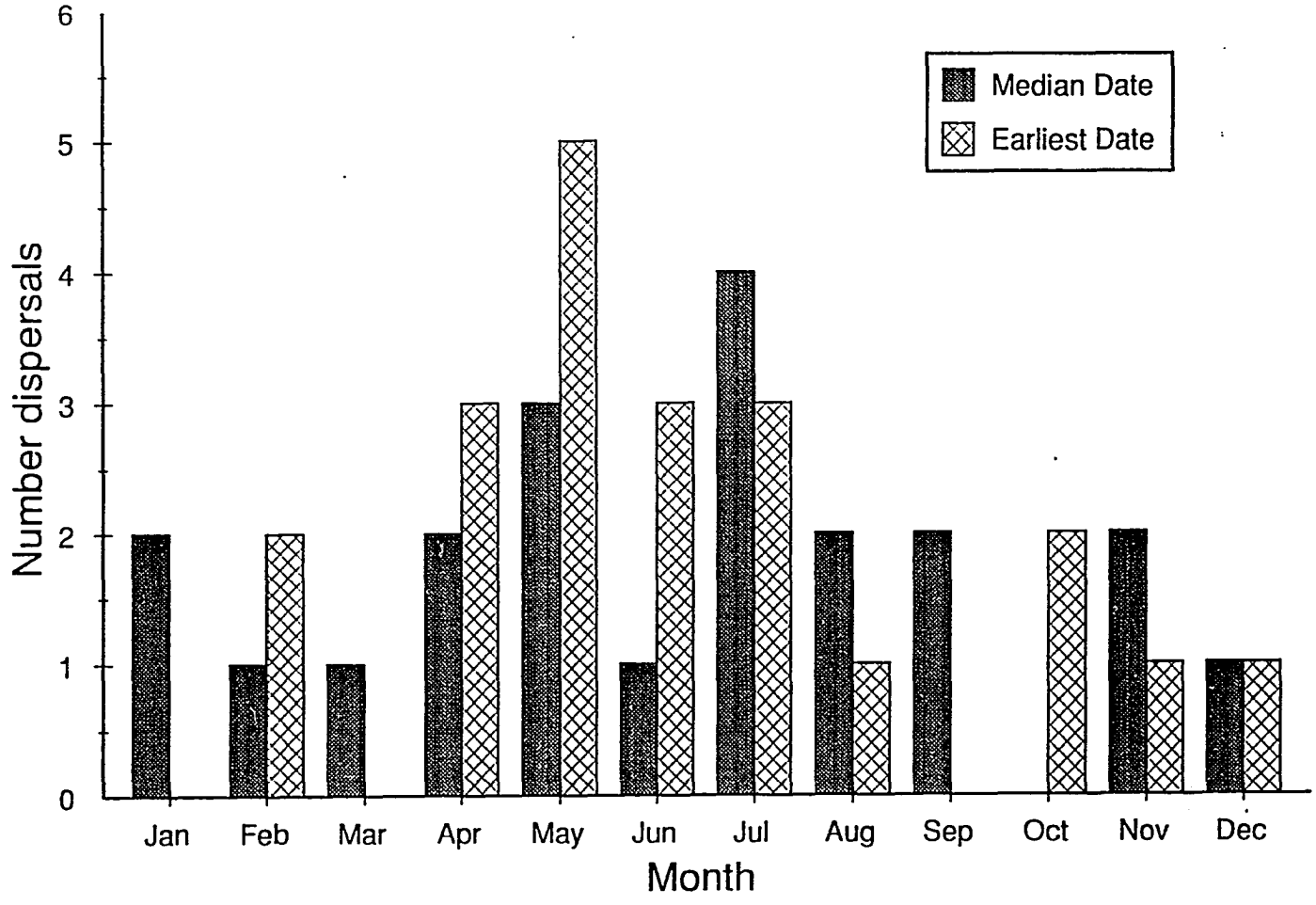


Fig 6. Timing of dispersal of wolves in northwest Alaska, April 1987 through July 1992.

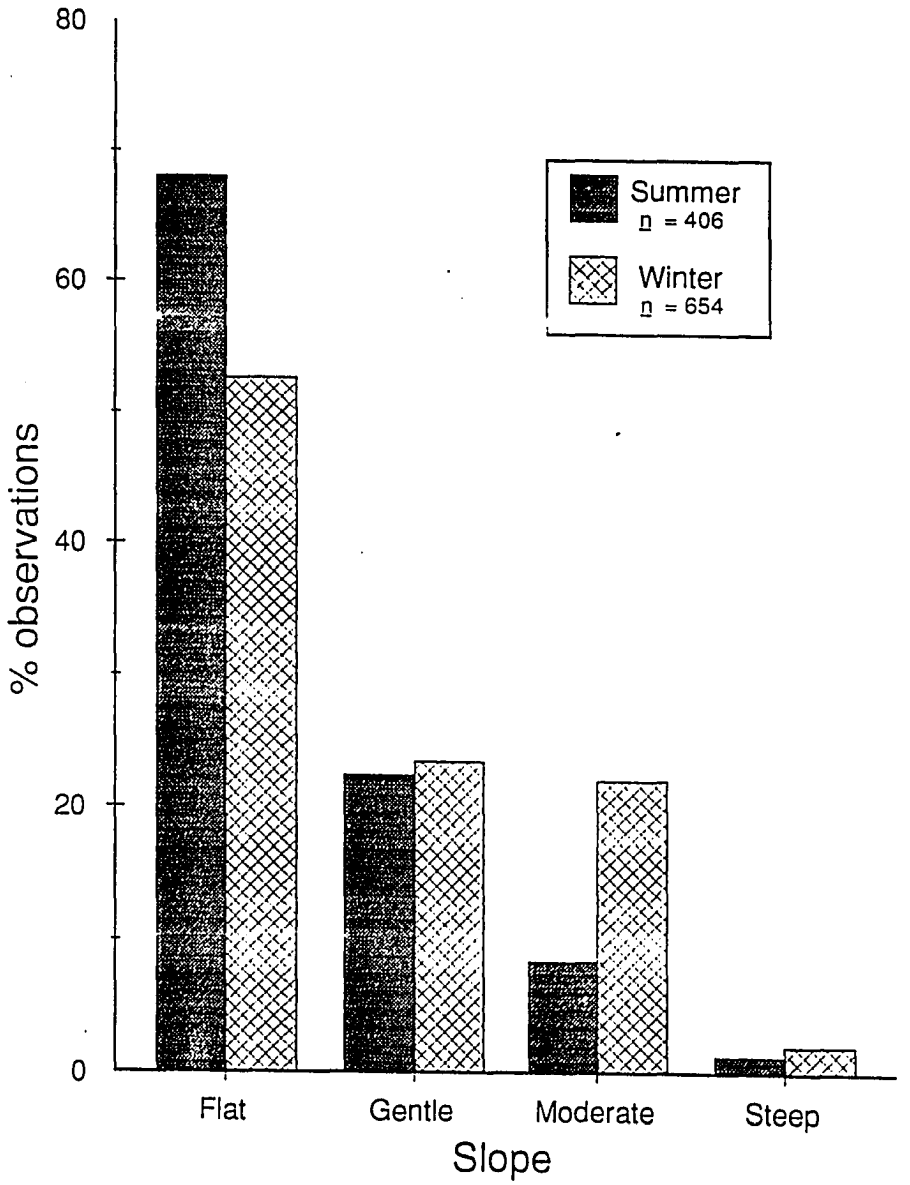


Fig. 7. Comparison of use of slopes (%) between summer and winter by radio-marked wolf packs in northwest Alaska, April 1987 through July 1992.

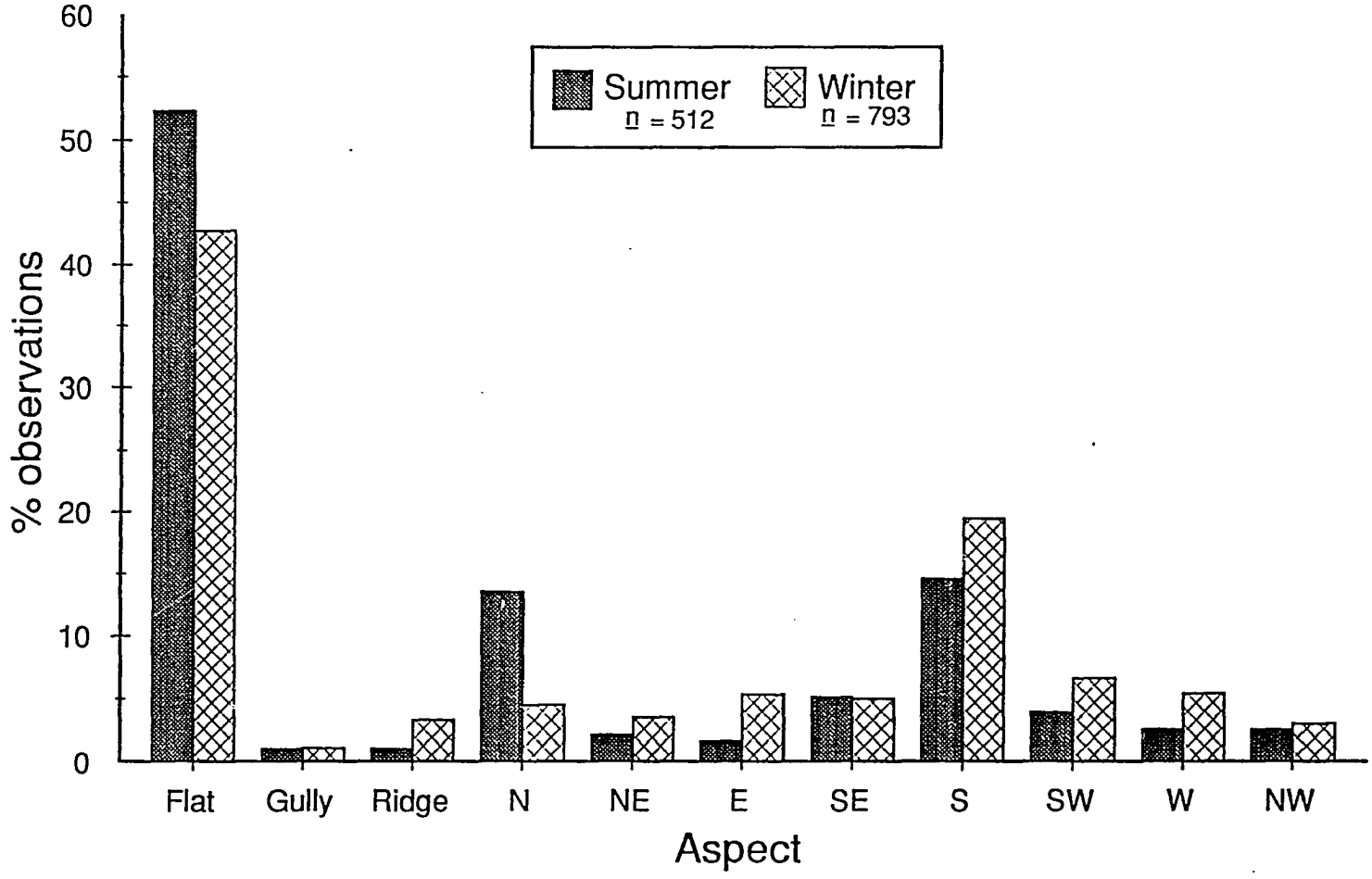
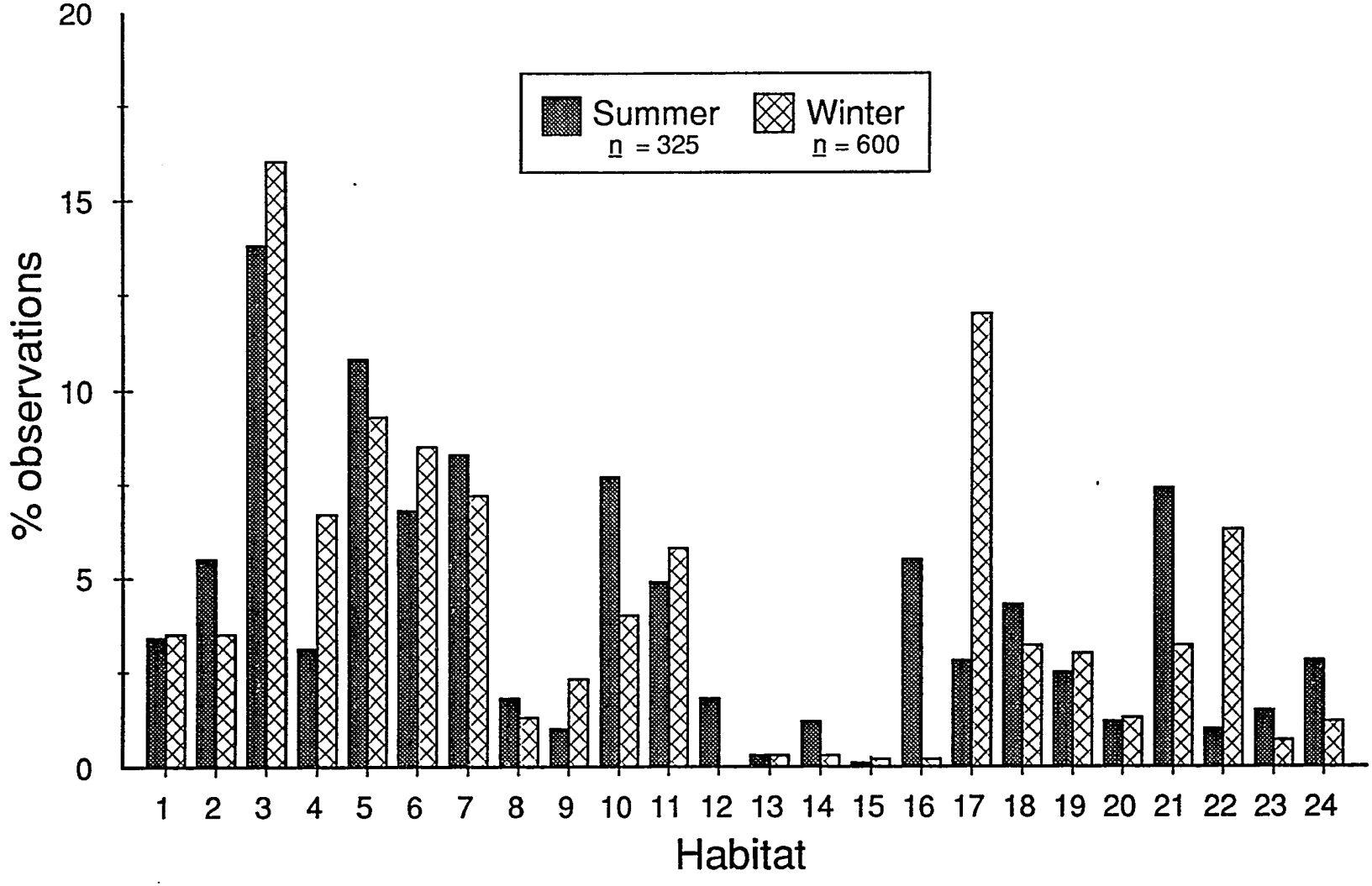


Fig. 8. Aspect use (% of obs) during summer and winter by radio-marked wolf packs in northwest Alaska, April 1987 through July 1992.

Fig. 9. Use of habitats (% of obs) by radio-marked wolf packs during summer and winter in northwest Alaska, April 1987 through July 1992. Habitats are coded as: 1 = sparse tall spruce, 2 = moderate tall spruce, 3 = dense tall spruce (usually riparian), 4 = sparse medium height spruce, 5 = moderate medium height spruce, 6 = dense medium height spruce, 8 = moderate low height spruce, 9 = dense low height spruce, 10 = shrubland, 11 = riparian willow, 12 = upland willow or shrub birch (Betula nana, B. glandulosa, and B. spp.), 13 = alder (Alnus spp.), 14 = tussock tundra, 15 = sedge-grass tundra, 16 = alpine herbaceous tundra, 17 = mat and cushion tundra, 18 = riparian hardwood, primarily cottonwood [Populus balsamifera]), 19 = mixed birch and spruce, 20 = birch, 21 = marsh, 22 = rock/ice/snow, 23 = gravel bar, and 24 = aspen (Populus tremeloides). Determination of spruce densities was subjective. Spruce heights were classified from fixed-wing aircraft as : low = 0.3 m, medium = 3-6.1 m, and tall >6.1 m.


Summer
n = 325
Winter
n = 600
% observations
0
5
10
15
20
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Habitat

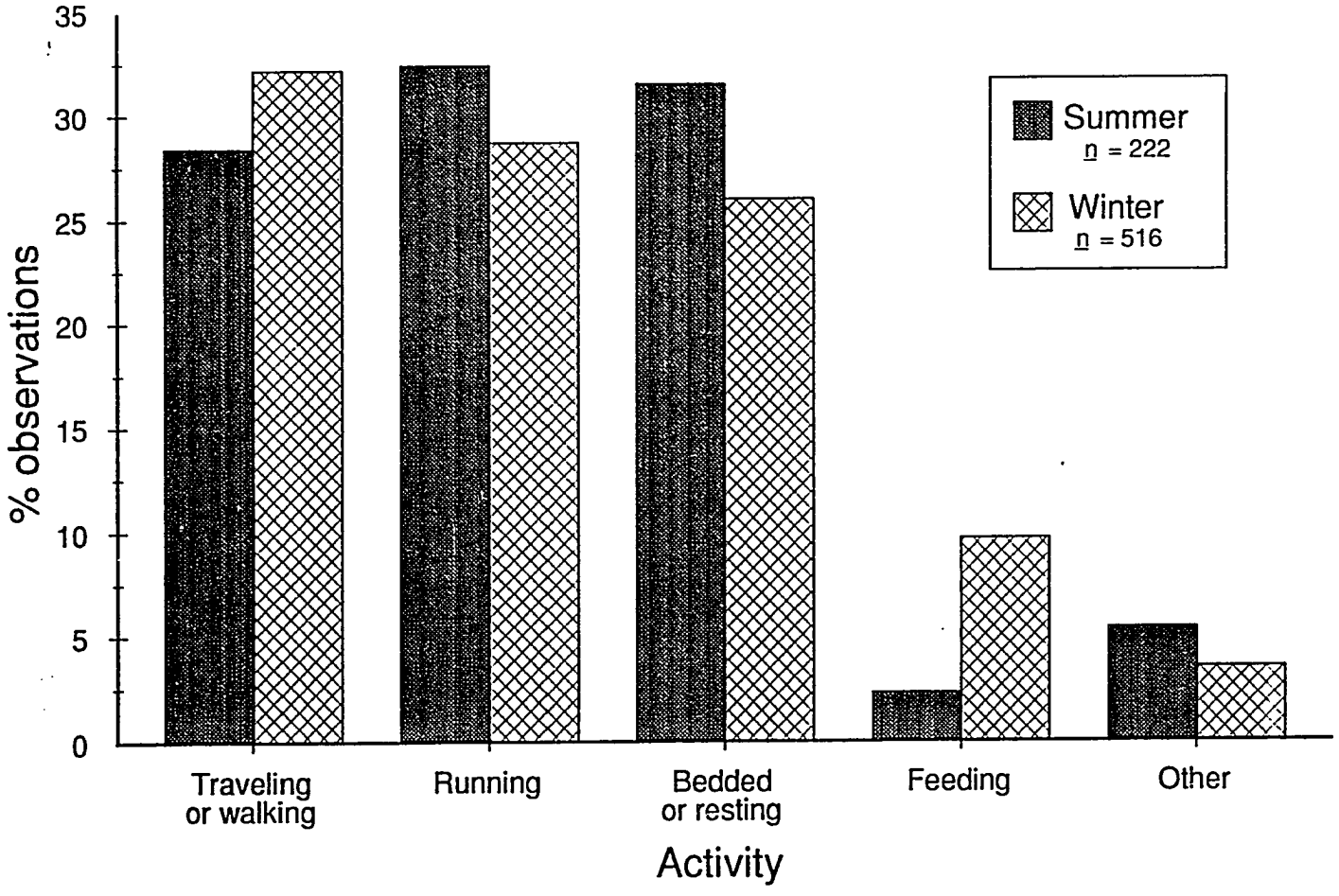


Fig. 10. Comparison of activity patterns (% of obs) between summer and winter for radio-marked wolf packs in northwest Alaska, April 1987 through July 1992.

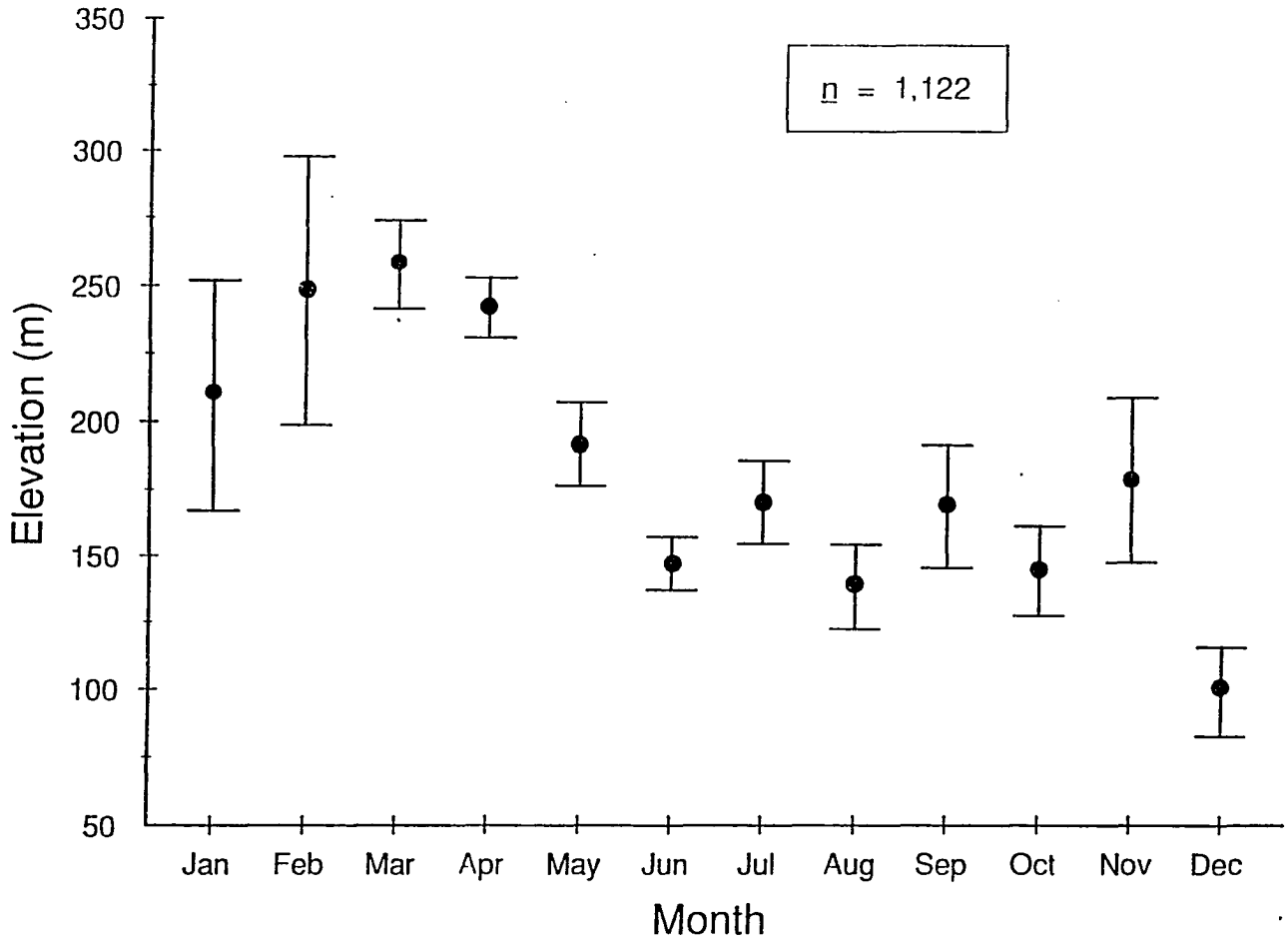


Fig. 11. Mean monthly elevations occupied by radio-marked wolf packs in northwest Alaska, April 1987 through July 1992. Error bars are ±1 SE.

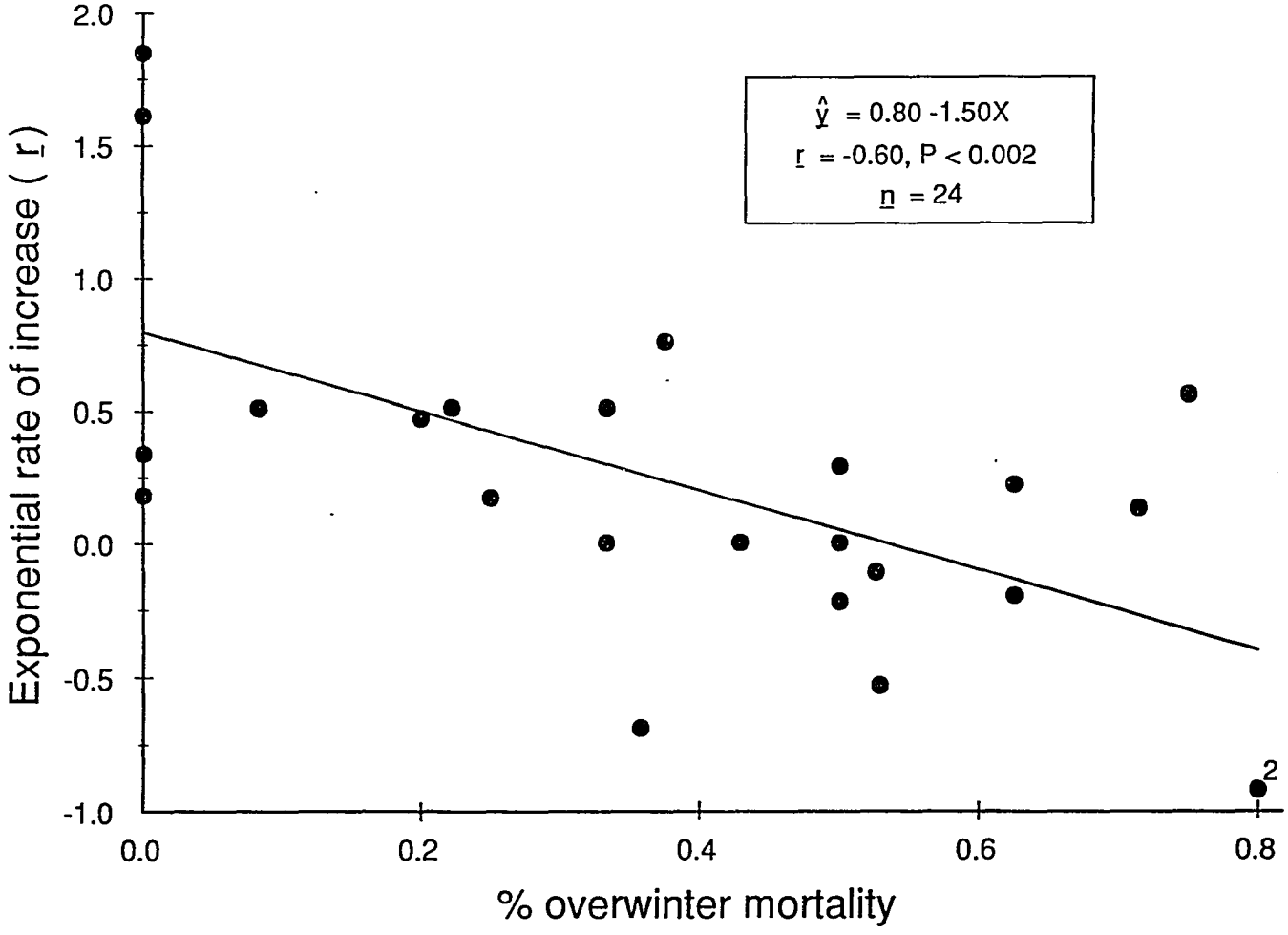


Fig. 12. Comparison of annual rates of mortality/wolf pack (autumn to spring) to exponential rates of increase (r from autumn to spring) for radio-marked wolf packs in northwest Alaska, autumn 1987 through autumn 1991.

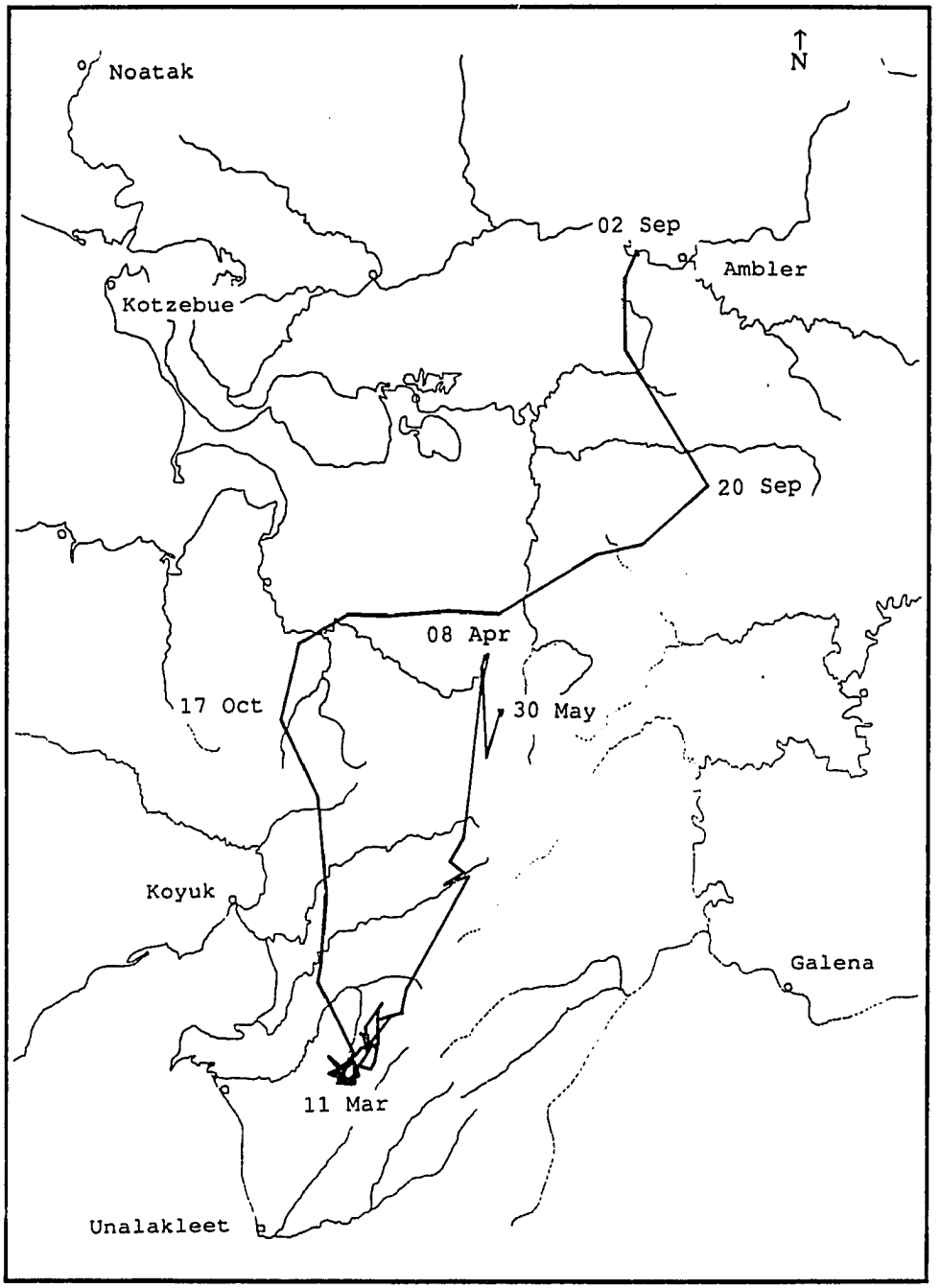


Fig. 13. Movements of adult female caribou satellite radio-collar no. 7870 in northwest Alaska, September 1989 through May 1990 (from Machida 1992).

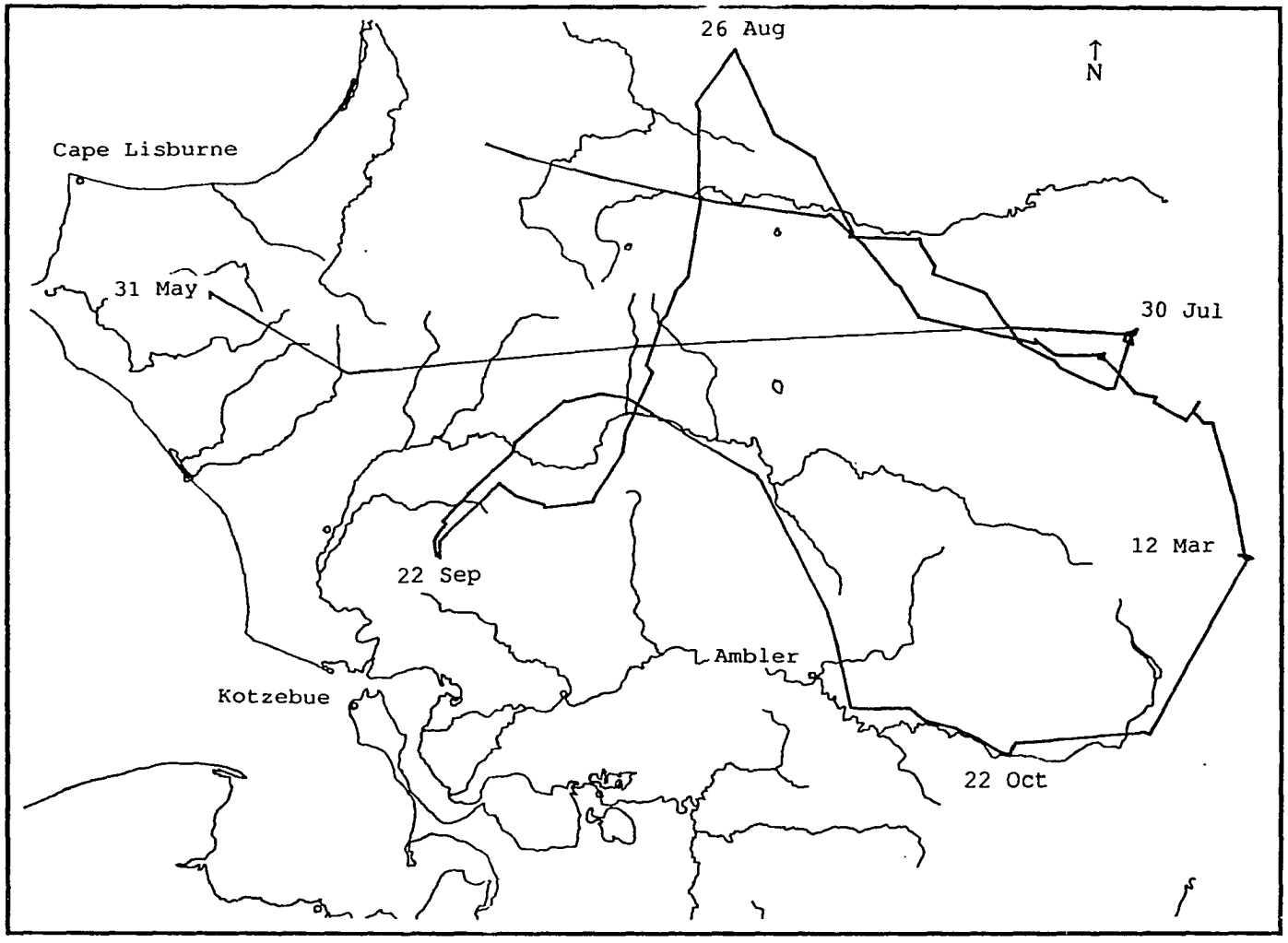


Fig. 14. Movements of adult female caribou satellite radio-collar no. 7871 in northwest Alaska, July 1989 through June 1990 (from Machida 1992).

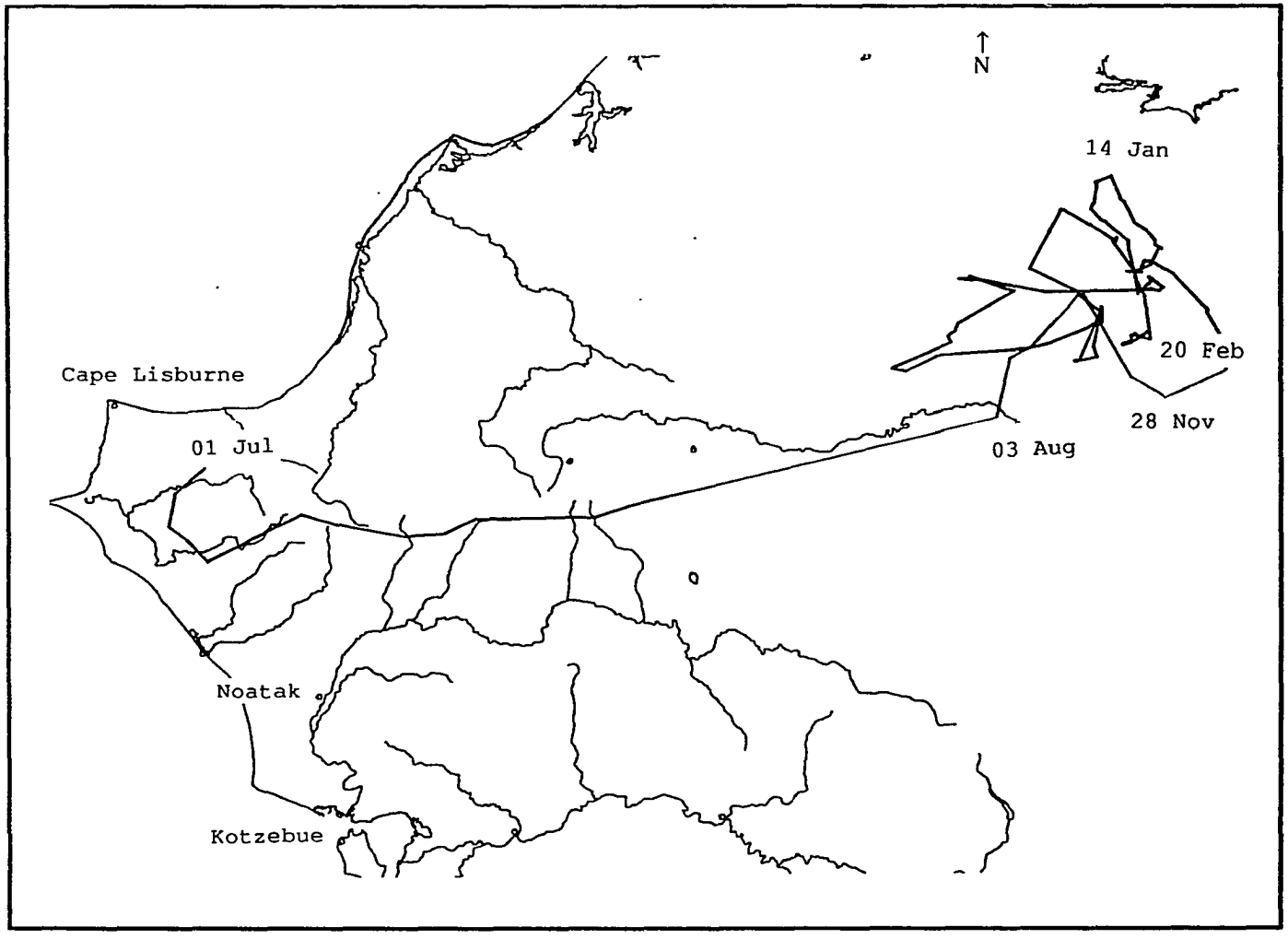


Fig. 15. Movements of adult female caribou satellite radio-collar no. 10906 in northwest Alaska, July 1989 through February 1990 (from Machida 1992).

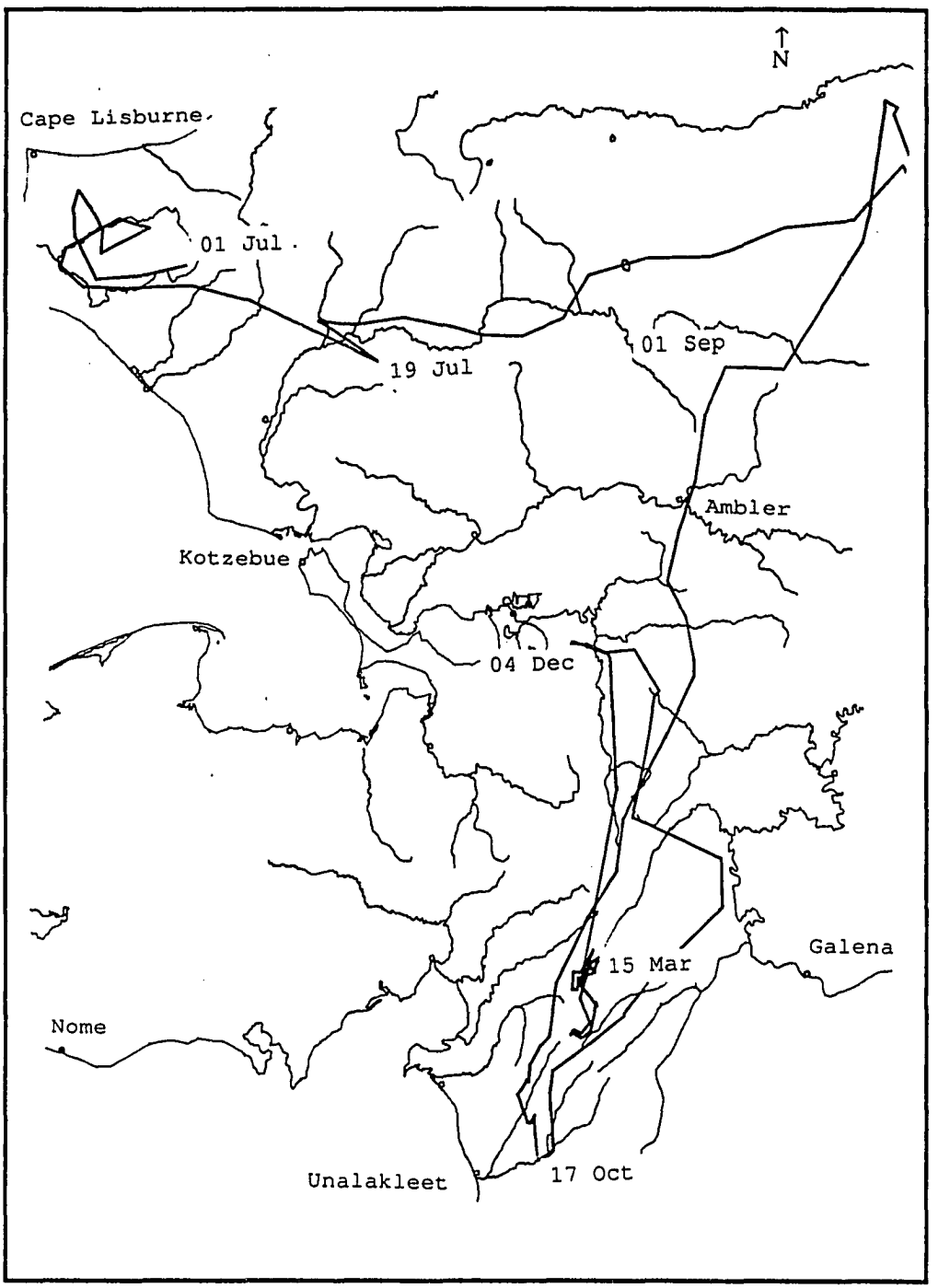


Fig. 16. Movements of adult female caribou satellite radio-collar no. 10907 in northwest Alaska, September 1989 through June 1990 (from Machida 1992).

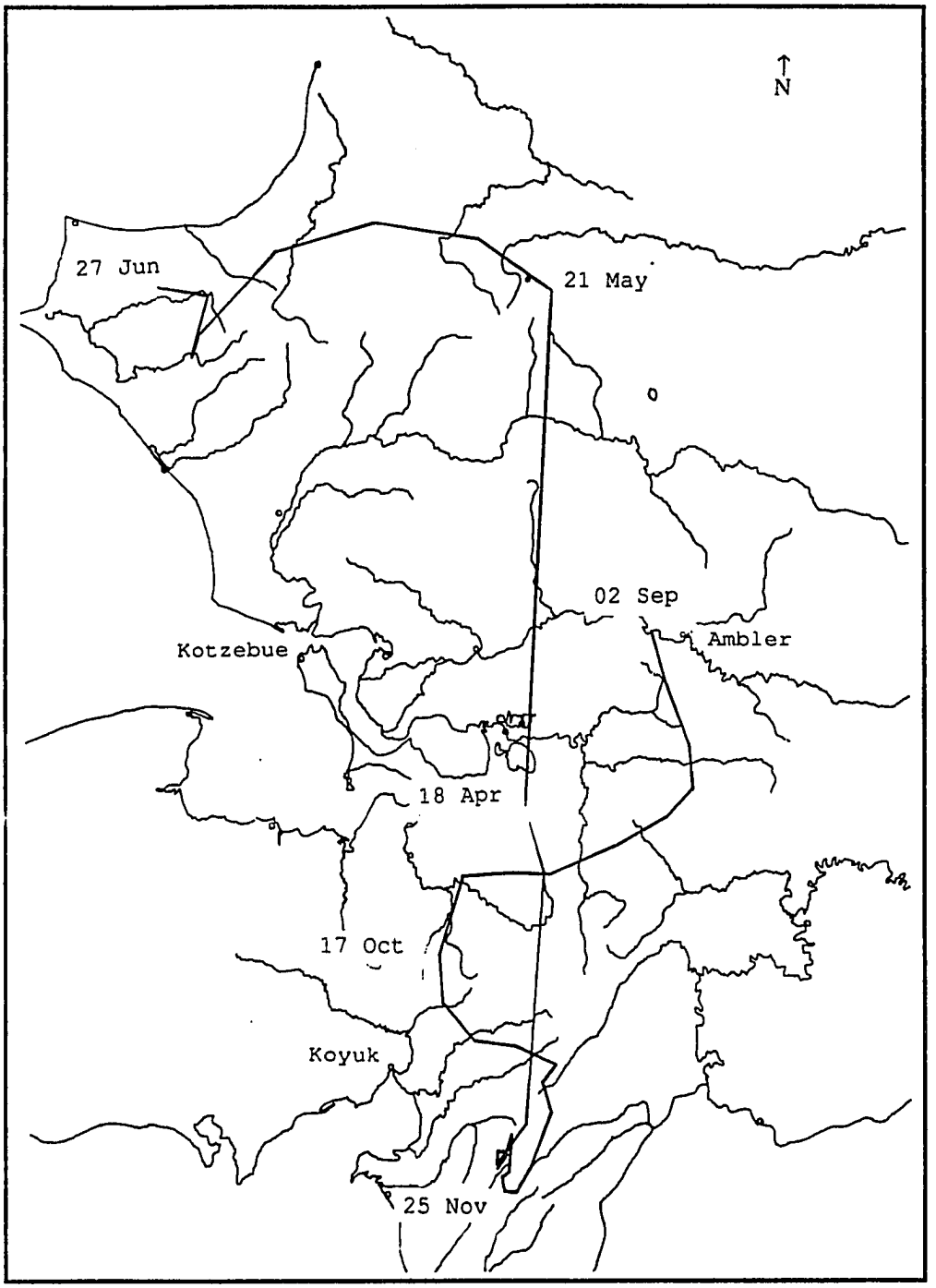


Fig. 17. Movements of adult female caribou satellite radio-collar no. 7871 in northwest Alaska, July 1988 through mid-March 1989 (from Machida 1992).

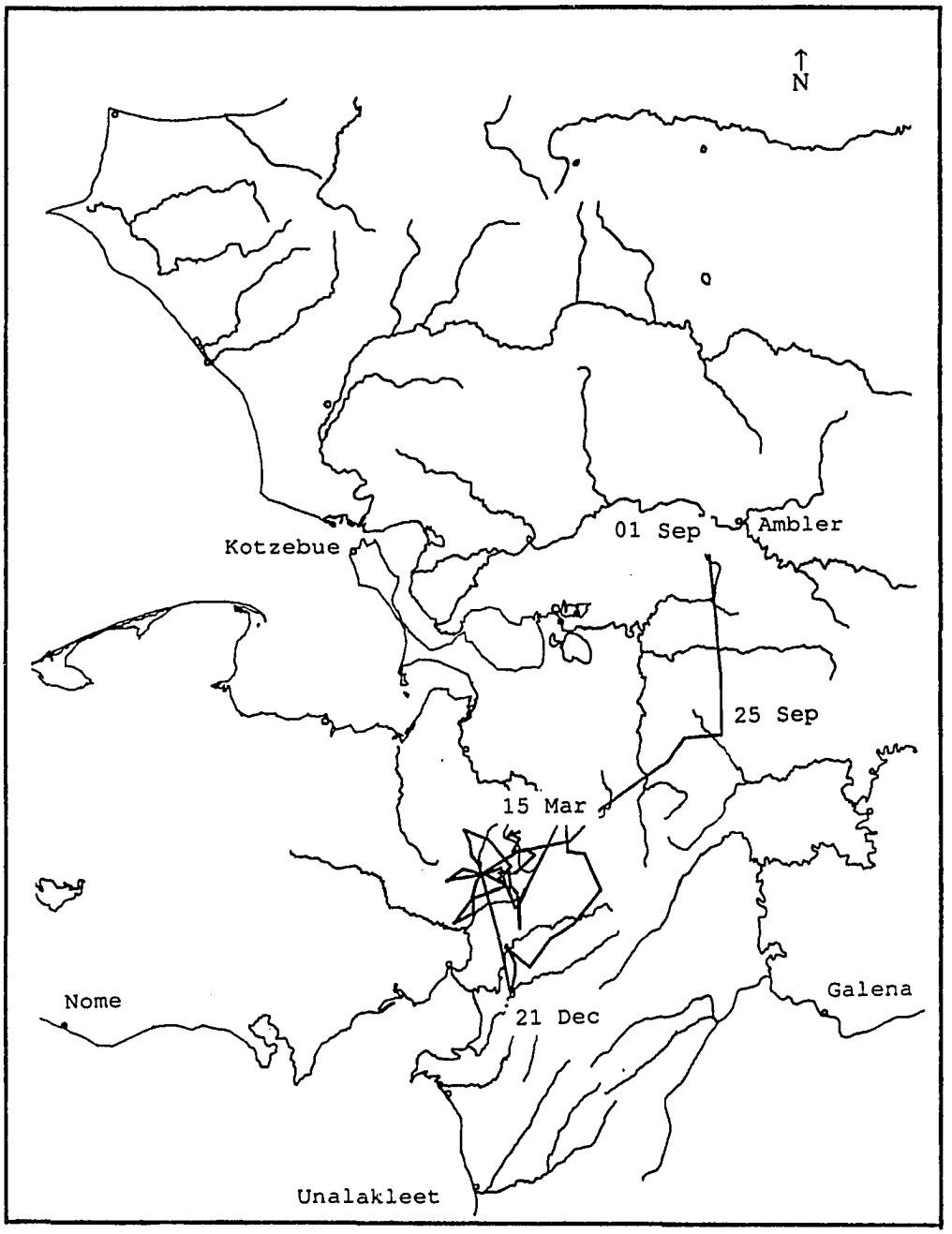


Fig. 18. Movements of adult female caribou satellite radio-collar no. 10906 in northwest Alaska, September 1988 through mid-March 1989 (from Machida 1992).

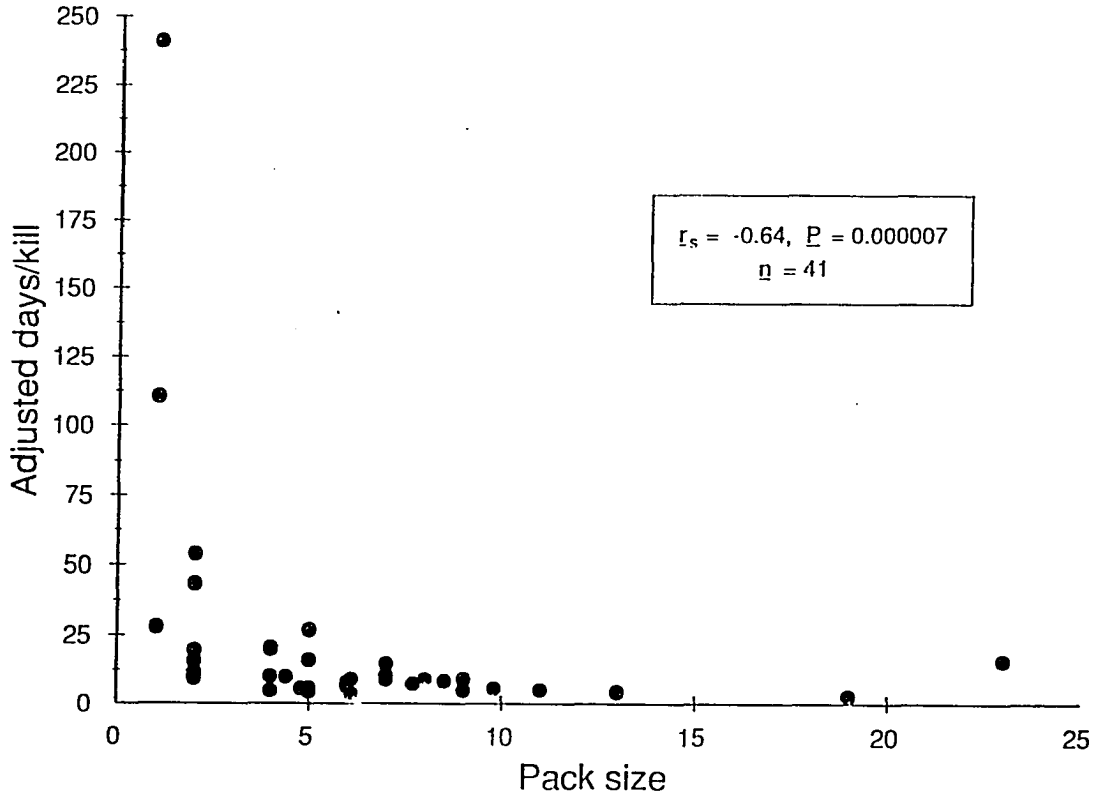


Fig. 19. Comparison of wolf pack sizes and adjusted kill rates (equivalent to 1 ad moose) for radio-marked wolf packs from several study areas within North America where caribou and moose were the principal prey species. Studies used in calculations include Ballard et al. (1987) from south-central Alaska, Hayes et al. (1991) from the Yukon Territory, and this study from northwest Alaska. Data sets were collected during March and April.

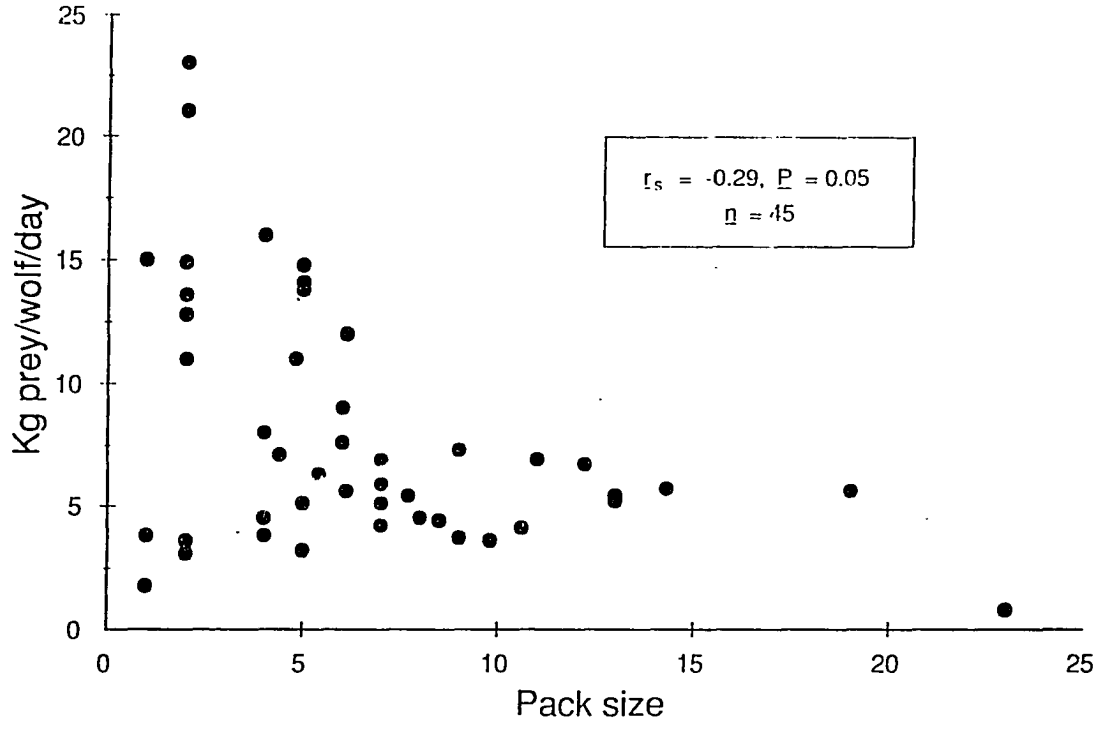


Fig. 20. Comparison of wolf pack sizes and kgs of prey weight/wolf/day from several study areas in North America where caribou and moose were the principal prey species. Studies used in calculations include Ballard et al. (1987) from south-central Alaska, Hayes et al. (1991) from the Yukon Territory, Dale et al. (1993) from Gates of the Arctic National Park, Alaska, and this study in northwest Alaska. Data sets were collected during March and April.

Table 1. Summary of wolves captured and radio-collared during 14 April, 1987 through 9 April, 1991, in northwest Alaska.

Pack	Dates immobilized	Sex	Age (Month)	Weight (kg)	Status on last contact	Month of last contact
1	15 Apr 87	M	35	43.1	Dead	Feb 88
2	15 Apr 87	F	23	44.0	Missing	Jul 89
	14 Apr 89		47	45.4		
2	15 Apr 87	M	35	49.9	Dead	Mar 91
2	15 Apr 87	F	11	34.0	Dead	Sep 89
7	14 Apr 89		35	39.9		
3	16 Apr 87	F	11		Dead	Jan 88
3	16 Apr 87	M	47		Dead	Jul 87
4	16 Apr 87	F	35	40.8	Dead	Apr 90
	24 Apr 88		47	37.6		
	10 Apr 89		59	39.0		
4	16 Apr 87	M	47	50.8	Dead	Jan 88
5	17 Apr 87	M	59	55.3	Dead	Feb 89
5	17 Apr 87	F	11		Dead	May 91
	26 Apr 88		23	47.6		
	10 Apr 89		35			
1	17 Apr 87	M	179		Dead	Jun 89
2	23 Mar 88	F	11	35.4	Missing	Jul 89
	11 Jun 88		13	33.1		
6	23 Apr 88	M	23	43.1	Dead	Mar 89
	13 Nov 88		30	42.6		
1	24 Apr 88	F	35	44.9	Dead	Mar 89
6	24 Apr 88	M	35	46.3	Dead	Mar 89
6	24 Apr 88	F	11	28.6	Dead	Mar 91
	15 May 90		35	36.3		

6	24 Apr 88	F	11	31.8	Dead	Dec 89
5	26 Apr 88	M	11	49.0	Missing	Jul 89
5	26 Apr 88 10 Apr 89	M	11 23	47.2 50.8	Dead	May 90
5	26 Apr 88 27 Apr 88	M	23 23	49.9	Dead	Apr 88
5 11	26 Apr 88 09 Apr 91	M	23 59	47.2	Dead or dropped collar	Aug 91
12	03 Aug 88 12 Nov 88	F	3 6	11.3 24.9	Dead	Dec 88
1	14 Nov 88	F	6		Dead	Jan 89
3	27 Jun 88 14 Nov 88	M	37 42	47.6 49.9	Dead	Feb 89
1	14 Nov 88	M	6	34.0	Dead	Mar 89
4	15 Nov 88	M	42	46.3	Dead	Mar 89
12	15 Nov 88	M	114	44.5	Missing	May 90
12	15 Nov 88	M	6	31.8	Dead	Dec 88
1	09 Apr 89	F	11	42.6	Dead	May 89
1	09 Apr 89	F	11	37.2	Dead	Feb 90
13	09 Apr 89	F	23	38.6	Dead	Aug 89
13	09 Apr 89 17 Apr 90	F	11 23	38.1 36.7	Dead	Jun 90
11	10 Apr 89 14 Apr 90	F	35 47	47.2 39.9	Dead	Mar 92
5	10 Apr 88	F	47	47.6	Dead	Jan 92
5	10 Apr 89	F	11		Missing	Apr 90
3	13 Apr 89	F	11	38.1	Missing	Feb 91

3	13 Apr 89	F	35	44.9	Missing	May 89
3	13 Apr 89	M	11	45.8	Dead	Jan 90
3	13 Apr 89	F	11		Missing	Apr 90
6	14 Apr 89	F	11	34.5	Missing	Mar 90
7	14 Apr 89	M	35	49.0	Dead	Feb 91
2	14 Apr 89	F	11	34.5	Dead	Mar 91
2	14 Apr 89	M	11	40.8	Dead	Mar 91
2	14 Apr 89	M	35	49.0	Missing	May 89
8	15 Apr 89	F	35	36.3	Missing	Sep 89
9	15 Apr 89	F	11	39.0	Alive	Oct 91
	15 Apr 90		23	44.5		
9	15 Apr 89	F	47	39.9	Alive	Oct 91
10	15 Apr 90	M	83	51.7	Missing	Jun 89
14	19 Apr 89	M	35	42.6	Dead	Mar 90
13	12 Apr 90	M	AD	40.4	Missing	Aug 90
7	12 Apr 90	F	11	44.5	Dead	Feb 91
5	13 Apr 90	F	11	38.1	Dead	May 90
5	13 Apr 90	F	11	43.1	Dead	Jul 90
5	13 Apr 90	M	11	43.5	Missing	May 90
5	13 Apr 90	F	23	46.7	Dead	May 90
5	13 Apr 90	F	11	37.2	Dead	May 90
15	13 May 90	F	47	50.3	Missing	Oct 90
15	13 Apr 90	F	11	39.5	Dead	Mar 91
15	13 Apr 90	M	35	47.6	Alive	Jul 92
15	13 Apr 90	M	23	44.9	Dead	Jan 91

15	13 Apr 90	F	23	40.8	Prob. Dead	Apr 91
2	14 Apr 90	M	11	37.2	Missing	May 91
2	14 Apr 90	F	11	39.0	Dead	Mar 91
2	14 Apr 90 08 Apr 91	F	AD	39.9	Missing	Aug 91
3	14 Apr 90	M	11	41.7	Missing	Oct 91
3	14 Apr 90	M	23	41.7	Alive	Jul 92
3	14 Apr 90	F	23	39.0	Dead	Jun 90
11	14 Apr 90	M	AD	47.2	Dead	May 91
11	14 Apr 90	M	23	45.4	Missing	Mar 91
16	18 Apr 90	M	47		Dead	Oct 90
9	15 Apr 90	M	119	54.4	Alive	Oct 91
9	15 Apr 90	F	23	39.0	Missing	Jun 90
9	15 Apr 90	M	35	48.1	Dead	Apr 91
6	15 Apr 90	M	35	49.4	Missing	Jul 90
6	15 Apr 90	M	11	41.7	Missing	Oct 90
16	18 Apr 90	F	47		Dead	Mar 91
5	07 Apr 91	F	35	43.1	Dead	Mar 92[b]
17	07 Apr 91	M	35	44.5	Alive	Jul 92
17	07 Apr 91	F	35	40.8	Alive	Jul 92
2	08 Apr 91	F	AD	46.7	Dead	Mar 92[b]
2	08 Apr 91	M	47		Dead or Dropped Collar	Jul 91
18	09 Apr 91	M	23	46.3	Alive	Oct 91

18	09 Apr 91	F	AD		Dead	Jun 91
5	09 Apr 91	M	23	44.5	Alive	Jul 92
19	09 Apr 91	M	11	49.0	Dead	Mar 92[b]
19	09 Apr 91	M	11	49.9	Dead	Dec 91

[a] Pack names: 1 = Rabbit Mt., 2 = Purcell Mt., 3 = Pick River, 4 = Jade Mt., 5 = Nuna Creek, 6 = Ingruksukruk, 7 = Huslia, 8 = Lower Tag., 9 = Upper Tagagawik, 10 = Kateel River, 11 = Dunes, 12 = Kiana, 13 = Kiliovilik, 14 = Anisak, 15 = Salmon River, 16 = Selawik River, 17 = Tutuksuk River, 18 = Lost Pack, and 19 = Cutler River.

[b] Exact date not reported.

Table 2a. Average weight by sex and age class of wolves captured in northwest Alaska, during April 1987 through 1991.

Age[a]	Sex	n	$\bar{x}$	SD
Ad	M	24	47.2	3.9
Ad	F	17	42.2	4.1
Yrl	M	8	46.2	3.1
Yrl	F	9	41.9	3.9
Pup	M	10	44.6	4.2
Pup	F	18	37.2	4.0

Table 2b. P-value for comparisons of weights of wolves captured in northwest Alaska, April 1987 through 1991.

Age	Sex	Ad M	Ad F	Yrl M	Yrl F	Pup M	Pup F
Ad	M	-	0.002	0.99	0.01	0.50	0.0001
Ad	F	0.002	-	0.20	0.99	0.67	0.004
Yrl	M	0.99	0.20	-	0.24	0.96	0.0001
Yrl	F	0.01	0.99	0.24	-	0.67	0.05
Pup	M	0.50	0.67	0.96	0.67	-	0.0002
Pup	F	0.0001	0.004	0.0001	0.05	0.0002	-

[a] Ad = > 2 Years; Yrl = Yearling, ≥ 12 and < 24 months; Pup = < 12 months.

Table 3. Summary of number of relocations and seasonal and total territory sizes (km^2) of radio-collared wolf packs in northwest Alaska, April 1987 through July 1992.

Pack Name	Summer territory		Winter territory		Total territory		No. relocations
	n	size	n	size	n	size	
Anisak	3	10	2	117	6	176	7
Cutler	4	108	3	11	6	108	6
Dunes	21	548	59	1,192	79	1,540	84
Huslia	12	996	16	1,777	27	2,350	27
Ingruksukruk	49	1,682	69	3,207	117	4,393	122
Jade Mt.	29	438	65	816	93	939	93
Kateel	3	17	4	129	6	174	6
Kiana	16	378	23	662	38	748	38
Kiliovilik	17	973	23	3,104	40	3,363	40
Lower Tag	8	174	2		9	245	9
Nuna Creek	69	5,774	134	3,262	202	7,031	209
Pick River	42	1,872	39	4,111	80	5,254	95
Purcell Mt.	65	1,827	118	2,670	182	3,211	183
Rabbit Mt.	38	1,140	78	2,850	115	3,195	118
Salmon River	9	323	11	786	19	809	23
Selawik River	6	135	9	310	14	377	14
Tutuksukruk	6	1,184	4	2,237	9	2,602	9
Upper Tag	17	635	19	1,749	35	1,807	36

Total[c]	414	18,214	678	28,990	1,077	38,322	1,119
$\bar{x}$	23	1,102	38	1,705	60	2,129	62
SD	21	1,300	40	1,278	59	1,928	61

[a] Excludes dispersals and long-distance movements to caribou winter range.

[b] Includes dispersals and long-distance movements to caribou range.

[c] Excludes Lost River pack due to inadequate no. relocations.

Table 4. Radio-collared wolf packs used to compare summer and winter territory sizes (km^2) and correlations between maximum pack sizes and territory sizes in northwest Alaska, 1987-1991.

Pack Name	Pack Size	Summer territory		Winter territory		Total territory	
		n	size	n	size	n	size
Dunes	6	21	548	59	1,192	79	1,540
Ingruksukruk	14	49	1,682	69	3,207	117	4,393
Jade Mt.	2	29	438	65	816	93	939
Nuna Creek	24	69	5,774	134	3,262	202	7,031
Pick River	17	42	1,872	39	4,111	80	5,254
Purcell Mt.	20	65	1,827	118	2,670	182	3,211
Rabbit Mt.	8	38	1,140	78	2,850	115	3,195
$\bar{x}$	13	44.7	1,897	80.3	2,587	124	3,652
SD	7.4	16.4	1,674	31.2	1,090	45.5	1,955

Table 5.Summary by sex and age class of wolf extra-territorial movements and dispersals in northwest Alaska, 1987 through 1991.

Pack Name-Wolf No.	Sex	Age (months)	Dispersal (km)	Dispersal dates		Status last obs
				Range	Median	
Dispersals						
Purcell Mt. - 4	F	49	16	24 Jun-21 Sep 1988	8 Aug	Paired
Pick River - 6	M	50	328	7 Jul-1 Nov 1987	3 Sep	Alone
Nuna Creek - 9	M	81	375	1 Feb 1989	1 Feb	Existing
Ingruksukruk - 17	F	22	77	22 Feb-4 Apr 1989	14 Mar	Paired
Nuna Creek - 18	M	26	64	1 Jul 1989	1 Jul	Missing
Nuna Creek - 21	M	25	64	3 Jun-17 Aug 1988	11 Jul	Paired
Kiana - 27	M	132	16	1 May 1990	1 May	Missing
Dunes - 33	F	47	106	18 Apr-28 Aug 1990	23 Jun	Missing
Nuna Creek - 35	F	22	166	2 Apr-7 Apr 1990	5 Apr	Missing
Pick River - 36	F	17	272	12 Oct 1990-11 Feb 1991	12 Dec	Missing
Pick River - 38	M	12	148	25 May-6 Sep 1989	16 Jul	Killed
Upper Tag - 46	F	18	113	16 Nov-27 Mar 1989	21 Jan	Alive
Salmon River - 57	F	49	154	21 Jun-12 Oct 1990	17 Aug	Missing
Salmon River - 59	M	35	64	1 May-14 May 1991	8 May	Alone
Pick River - 65	M	23	135	1 May 1990	1 May	Alone
Pick River - 66	M	36	77	14 May-28 Aug 1991	6 Jul	Alone
Dunes - 68	M	AD	270	20 Jul 1990-11 Mar 1991	14 Nov	Killed

Dunes - 69	M	31	166	5 Dec 1990-3 Mar 1991	18 Jan	Missing
Tutuksuk River - 80	F	39	72	28 Aug-1 Oct 1991	14 Sep	With pups
Lost River - 83	M	23	142	9 Apr-10 May 1991	24 Apr	Alone
Cutler River - 87	M	17	154	8 Oct-15 Dec 1991	16 Nov	Killed
Followed Caribou						
Ingruksukruk - 13	M	34	167	22 Feb-4 Apr 1989		Killed
Ingruksukruk - 15	M	46	167	22 Feb-4 Apr 1989		Killed
Ingruksukruk - 17	F	30	64	6 Nov-1 Dec 1989		Killed
Rabbit Mt. - 25	M	6	264	14 Nov-10 Mar 1989		Killed
Anisak - 49	M	41	85	28 Nov-24 Feb 1990		Killed
Pick River - 65	M	17	272	12 Oct 1990-14 Apr 1991		Missing
Pick River - 66	M	29	272	12 Oct 1990-14 May 1991		Missing

Table 6. Observed number of wolves within radio-collared wolf packs during spring and autumn 1987 through 1991 used to estimate wolf densities and population size in northwest Alaska and Game Management Unit (GMU) 23. Underlined pack names were used for density estimates.

	No. wolves									
Pack Name	Spr 87	Aut 87	Spr 88	Aut 88	Spr 89	Aut 89	Spr 90	Aut 90	Spr 91	Aut 91
Anisak	--	--	--	--	2	3	--	--	--	--
Cutler River	--	--	--	--	--	--	--	--	8	10
Dunes	0	0	0	1	2	5	5	6	1-2[a]	?
Huslia	--	--	--	1	2	4+	1	7	0	--
Ingruksukruk	4[a]	10[a]	10	14	9	7	4	7	0	--
Jade Mt.	2	2	1	2	1	2	0	0	0	--
Kiana	--	--	--	8	3	10	1	--	--	--
Kiliovilik	3[a]	3[a]	3[a]	3[a]	2	2	2	0	0	--
Lost River	--	--	--	--	--	--	--	--	4[b]	1
Lower Tag	--	--	--	--	2	3	--	--	--	--
Nuna Creek	8	9	7	15	12	24	16	3	3	19
Pick River	4	6	3	8	5	17	8	10	2	4
Purcell Mt.	6	12	11	20	10	16	12	19	9	6
Rabbit Mt.	3	7	2	8	3	1	0	--	--	--
Salmon River	--	--	--	--	--	--	10	19	8	--
Selawik River	--	--	--	--	--	--	2	2	2	--
Upper Tag	--	--	--	--	4	9	6	15	10	15
Subtotal (Used for density)	30 (30)	49 (49)	37 (37)	80 (71)	57 (44)	103 (74)	67 (49)	88 (47)	47-48 (17-18)	55 (29)

No. lone wolves assumed at 10%	3	5	4	7	4	7	5	5	2	3
Total	33	54	41	77	44	81	54	52	19–20	32
Size of study area (km^2)	12,279	12,279	12,279	12,279	12,279	12,279	12,279	12,279	12,279	12,279
Km^2/wolf	372	227	229	159	279	152	227	236	646–614	384
Wolves/ 1,000 Km^2	2.7	4.4	3.3	6.3	3.6	6.6	4.4	4.2	1.5–1.6	2.6
GMU 23 population estimate (assuming 119,140 km^2)	322	524	393	750	429	786	525	500	179–191	310
Spring finite rate increase			1.22		1.09		1.22		0.34 -0.36	
Autumn finite rate increase				1.43		1.05		0.64		0.62

[a] Estimates based on track counts, public obs. and harvest records.

[b] Could have been remnants of Salmon River pack.

Spr = Spring

Aut = Autumn

Table 7. Observed annual wolf litter sizes in northwest Alaska, 1987-1991.

Year	No. litters	$\bar{x}$ litter size	SD	Range
1987	4	3.5	1.12	2-7
1988	6	6.0	1.00	5-8
1989	5	5.4	2.80	2-10
1990	5	6.4	1.50	5-9
1991	2	4.0	0.00	0

Table 8. Monthly and annual survivorship of radio-collared yearling female wolves in northwest Alaska, 1987–88 through 1990–91 using Kaplan-Meier procedures (Pollock et al. 1989).

Month	1987–1988		1988–1989		1989–1990		1990–1991		Pooled			Mean	
	n	Rate	n	Rate	n	Rate	n	Rate	n	Rate	95%CI	n	Rate	95%CI
May	4	1.000	3	1.000	9	0.889	6	0.667	22	0.864	0.730–0.997	5.5	0.889	0.764–1.014
Jun	4	1.000	3	1.000	8	0.889	4	0.667	19	0.864	0.720–1.007	4.75	0.889	0.745–1.034
Jul	4	1.000	3	1.000	8	0.889	4	0.500	19	0.818	0.661–0.975	4.75	0.847	0.710–0.985
Aug	4	1.000	3	1.000	8	0.889	3	0.500	18	0.818	0.657–0.979	4.50	0.847	0.696–0.999
Sep	4	1.000	3	1.000	8	0.889	3	0.500	18	0.818	0.657–0.979	4.50	0.847	0.696–0.999
Oct	4	1.000	3	1.000	8	0.889	3	0.500	18	0.818	0.657–0.979	4.50	0.847	0.696–0.999
Nov	4	1.000	3	1.000	8	0.889	3	0.500	18	0.818	0.657–0.979	4.50	0.847	0.696–0.999
Dec	4	1.000	3	1.000	8	0.778	3	0.500	18	0.773	0.603–0.943	4.50	0.820	0.656–0.983
Jan	4	0.750	3	1.000	7	0.778	3	0.333	17	0.682	0.500–0.865	4.25	0.715	0.479–0.952
Feb	3	0.750	3	1.000	7	0.778	2	0.167	15	0.636	0.442–0.831	3.75	0.674	0.447–0.900
Mar	3	0.750	3	1.000	7	0.778	1	0.000	14	0.591	0.391–0.789	3.50	0.632	0.458–0.806
Apr	3	0.750	3	1.000	6	0.778	0	0.000	12	0.591	0.377–0.805	3.00	0.632	0.453–0.811

Table 9. Monthly and annual survivorship of radio-collared yearling male wolves in northwest Alaska, 1988-89 through 1991-92 using Kaplan-Meier procedures (Pollock et al. 1989).

Month	1988-1989		1989-1990		1990-1991		1991-1992		Pooled			Mean		
	n	Rate	n	Rate	n	Rate	n	Rate	n	Rate	95%CI	n	Rate	95%CI
May	2	1.000	2	1.000	4	1.000	2	1.000	10	1.000	1.000	2.50	1.000	1.000
Jun	2	1.000	2	1.000	3	1.000	2	1.000	9	1.000	1.000	2.25	1.000	1.000
Jul	2	1.000	2	1.000	3	1.000	2	1.000	9	1.000	1.000	2.25	1.000	1.000
Aug	2	1.000	2	1.000	3	1.000	2	1.000	9	1.000	1.000	2.25	1.000	1.000
Sept	2	1.000	2	1.000	3	1.000	2	1.000	9	1.000	1.000	2.25	1.000	1.000
Oct	2	1.000	2	1.000	3	1.000	2	1.000	9	1.000	1.000	2.25	1.000	1.000
Nov	2	1.000	2	1.000	2	1.000	2	1.000	8	1.000	1.000	2.00	1.000	1.000
Dec	2	1.000	2	1.000	2	1.000	2	1.000	8	1.000	1.000	2.00	1.000	1.000
Jan	2	1.000	2	1.000	2	1.000	2	0.500	8	0.750	0.490-1.010	2.00	0.875	0.503-0.995
Feb	2	1.000	1	0.500	2	1.000	1	0.500	6	0.750	0.450-1.050	1.50	0.750	0.404-1.100
Mar	2	1.000	1	0.500	2	1.000	1	0.500	6	0.750	0.450-1.050	1.50	0.750	0.404-1.100
Apr	2	1.000	1	0.500	2	1.000	1	0.000	6	0.625	0.319-0.931	1.50	0.625	0.452-0.798

Table 10. Monthly and annual survivorship of radio-collared adult (>24 mos.) female wolves in northwest Alaska, 1987-88 through 1991-92 using Kaplan-Meier procedures (Pollock et al. 1989).

Mos	1987-1988		1988-1989		1989-1990		1990-1991		1991-1992		Pooled			Mean		
	n	Rate	n	Rate	n	Rate	n	Rate	n	Rate	n	Rate	95%CI	n	Rate	95%CI
May	1	1.000	4	1.000	11	1.000	13	0.846	7	0.857	36	0.917	0.830-1.003	7.20	0.941	0.857-1.025
Jun	1	1.000	4	1.000	10	1.000	11	0.769	6	0.857	32	0.880	0.785-0.991	6.40	0.925	0.830-1.021
Jul	1	1.000	4	1.000	10	1.000	9	0.769	6	0.857	30	0.880	0.782-0.994	6.00	0.925	0.825-1.025
Aug	1	1.000	4	1.000	8	0.875	9	0.769	6	0.857	28	0.856	0.736-0.977	5.60	0.900	0.757-1.043
Sep	1	1.000	4	1.000	7	0.750	9	0.769	5	0.857	26	0.823	0.690-0.956	5.20	0.875	0.715-1.036
Oct	1	1.000	4	1.000	5	0.750	9	0.769	5	0.857	24	0.823	0.685-0.962	4.80	0.875	0.704-1.046
Nov	1	1.000	4	1.000	5	0.750	8	0.769	5	0.857	23	0.823	0.682-0.965	4.60	0.875	0.701-1.049
Dec	1	1.000	4	1.000	5	0.750	8	0.769	5	0.857	23	0.788	0.639-0.936	4.60	0.875	0.701-1.049
Jan	1	1.000	4	1.000	5	0.600	8	0.769	5	0.857	22	0.788	0.636-0.939	4.60	0.845	0.671-1.020
Feb	1	1.000	4	1.000	4	0.600	8	0.769	5	0.857	22	0.788	0.636-0.939	4.40	0.845	0.663-1.028
Mar	1	1.000	4	1.000	4	0.600	7	0.330	5	0.514	21	0.563	0.403-0.722	4.20	0.689	0.512-0.866
Apr	1	1.000	4	1.000	4	0.450	3	0.330	3	0.514	15	0.525	0.342-0.708	3.00	0.659	0.451-0.866

Table 11. Monthly and annual survivorship of radio-collared adult (>24 mos) male wolves in northwest Alaska, 1987–88 through 1991–92 using Kaplan-Meier procedures (Pollock et al. 1989).

Mos	1987–1988		1988–1989		1989–1990		1990–1991		1991–1992		Pooled			Mean		
	n	Rate	n	Rate	n	Rate	n	Rate	n	Rate	n	Rate	95%CI	n	Rate	95%CI
May	6	1.000	9	1.000	12	1.000	19	0.947	12	1.000	58	0.983	0.950–1.016	11.60	0.989	0.970–1.009
Jun	6	1.000	9	1.000	10	0.900	17	0.947	11	1.000	53	0.964	0.915–1.013	10.60	0.969	0.914–1.025
Jul	6	1.000	9	1.000	9	0.900	17	0.947	11	1.000	52	0.964	0.915–1.014	10.40	0.969	0.912–1.027
Aug	6	1.000	9	1.000	8	0.900	16	0.947	10	1.000	49	0.964	0.913–1.015	9.80	0.969	0.909–1.030
Sep	6	1.000	9	1.000	8	0.900	15	0.884	9	1.000	47	0.944	0.880–1.008	9.40	0.957	0.887–1.026
Oct	6	1.000	9	1.000	8	0.900	14	0.884	9	1.000	46	0.944	0.879–1.008	9.20	0.957	0.886–1.028
Nov	6	0.833	9	1.000	8	0.900	14	0.884	8	1.000	45	0.923	0.848–0.998	9.00	0.923	0.798–1.049
Dec	5	0.833	11	1.000	8	0.900	14	0.821	8	1.000	46	0.903	0.821–0.984	9.20	0.911	0.775–1.046
Jan	5	0.667	11	1.000	8	0.900	13	0.758	8	0.875	45	0.843	0.745–0.940	9.00	0.840	0.650–1.030
Feb	4	0.500	11	0.636	8	0.900	12	0.695	7	0.875	42	0.722	0.607–0.837	8.40	0.721	0.478–0.965
Mar	3	0.500	7	0.455	8	0.788	11	0.505	7	0.750	36	0.582	0.459–0.705	7.20	0.600	0.304–0.877
Apr	3	0.500	5	0.455	7	0.788	7	0.433	6	0.750	28	0.561	0.423–0.699	5.60	0.585	0.266–0.886

Table 12. Monthly and annual survivorship of radio-collared wolves (yearlings and adults) in northwest Alaska, 1987-88 through 1991-92 using Kaplan-Meier procedures[a].

Mos	1987-1988		1988-1989		1989-1990		1990-1991		1991-1992		Pooled			Mean		
	n	Rate	n	Rate	n	Rate	n	Rate	n	Rate	n	Rate	95%CI	n	Rate	95%CI
May	11	1.000	18	1.000	34	0.971	42	0.881	21	0.952	126	0.944	0.906-0.983	25.20	0.961	0.914-1.008
Jun	11	1.000	18	1.000	30	0.938	35	0.856	19	0.952	113	0.928	0.882-0.974	22.60	0.949	0.892-1.006
Jul	11	1.000	18	1.000	29	0.938	33	0.830	19	0.952	110	0.919	0.871-0.968	22.00	0.944	0.885-1.003
Aug	11	1.000	18	1.000	26	0.902	31	0.830	18	0.952	104	0.911	0.858-0.963	20.80	0.937	0.872-1.002
Sep	11	1.000	18	1.000	25	0.866	30	0.802	16	0.952	100	0.892	0.835-0.950	20.00	0.924	0.854-0.995
Oct	11	1.000	18	1.000	23	0.866	29	0.802	16	0.952	97	0.892	0.834-0.951	19.40	0.924	0.853-0.996
Nov	11	0.909	18	1.000	23	0.866	27	0.802	15	0.952	94	0.883	0.822-0.944	18.80	0.906	0.780-1.012
Dec	10	0.909	20	1.000	23	0.828	27	0.773	15	0.952	95	0.855	0.789-0.920	19.00	0.892	0.782-1.004
Jan	10	0.727	20	1.000	22	0.753	26	0.713	15	0.825	92	0.790	0.716-0.864	18.60	0.804	0.661-0.947
Feb	8	0.636	20	0.800	20	0.753	24	0.654	13	0.825	85	0.725	0.644-0.806	17.00	0.734	0.548-0.919
Mar	7	0.636	16	0.700	20	0.715	21	0.405	13	0.635	77	0.593	0.509-0.678	15.40	0.618	0.422-0.815
Apr	7	0.636	14	0.700	18	0.676	12	0.371	10	0.571	61	0.564	0.470-0.657	12.20	0.591	0.379-0.803

[a] Excludes 4 pups < 12 mos. old.

Table 13. P values for comparisons of annual survivorship of radio-collared wolves by sex-age class in northwest Alaska during 1987-88 through 1990-91.

Age	Sex	Year	1988-89	1989-90	1990-91	1991-92
Yearling	Female	1987-88	0.332	0.919	0.041	
		1988-89		0.176	0.000	
		1989-90			0.0008	
Yearling	Male	1988-89		0.392	1.000	0.000
		1989-90			0.392	0.392
		1990-91				0.000
Adult	Female	1988-89		0.008	0.001	0.057
		1989-90			0.604	0.813
		1990-91				0.489
Adult	Male	1987-88	0.862	0.270	0.785	0.350
		1988-89		0.120	0.911	0.185
		1989-90			0.065	0.855
		1990-91				0.120
Pooled		1987-88	0.724	0.821	0.132	0.732
		1988-89		0.860	0.018	0.416
		1989-90			0.016	0.488
		1990-91				0.176

Table 14. Fates of 86 radio-collared wolves and cause-specific mortality rates in northwest Alaska, April 1987 through April 1992[ab].

Year	Alive on 30 Apr 92	Missing	Dead or Dropped Collar	Hunting		Starvation	Wolf Predation	Rabies	Old Age	Total
				Snow-machine	Aircraft					
1987-88	0	0	0	4	0	0	0	0	0	4
1988-89	0	0	0	9	2	0	0	0	0	11
1989-90	2	10	0	4	0	0	1	2	1	20
1990-91	3	9	0	11	0	3	0	8	0	34
1991-92	4	3	2	6	0	0	0	1	0	16
Total	9	22	2	34	2	3	1	11	1	85
%	10.6	25.9	2.4	40.0	2.4	3.5	1.2	12.9	1.2	100.1
Mortality Rate				0.410	0.024	0.036	0.012	0.133	0.012	

[a] One wolf sacrificed shortly after capture in April 1988 not included.

[b] Cause-specific mortality rates calculated using methods described by Heisey and Fuller (1985).

Table 15. Timing of mortality or month when radio contact was lost with radio-collared wolves in northwest Alaska, April 1987 through April 1992[a].

Month	Hunting		Rabies	Starved	Wolf Predation	Old age	Missing[b]		Total	
	Snow-machine	Air-craft					n	%	n	%
May	1	0	6	0	0	0	6	25.0	13	17.1
Jun	0	0	1	0	0	1	1	4.2	3	3.9
Jul	0	0	1	0	0	0	5	20.8	6	7.9
Aug	0	0	1	0	0	0	3	12.5	4	5.3
Sep	0	0	1	0	1	0	1	4.2	3	3.9
Oct	0	0	0	0	0	0	3	12.5	3	3.9
Nov	1	0	0	0	0	0	0	0	1	1.3
Dec	5	0	1	0	0	0	0	0	6	7.9
Jan	6	0	0	1	0	0	0	0	7	9.2
Feb	5	2	0	0	0	0	1	4.2	8	10.5
Mar	14	0	0	2	0	0	2	8.3	18	23.7
Apr	2	0	0	0	0	0	2	8.3	4	5.3
Total	34	2	11	3	1	1	24	100.0	76	99.9

[a] Excludes sacrificed wolf.

[b] Dead or dropped collar counted as missing.

Table 16. Occurrence of rabies in northwest Alaska within selected canine species as reported by the Alaska Public Health Laboratory in Fairbanks, Alaska, 1971-1992 (From D. G. Ritter, State Public Health Laboratory, Fairbanks, pers. commun.).

		Arctic Fox			Red Fox			Wolves		Dogs			
Year	GMU	22	23	26	22	23	26	23	26	22	23	26	Total
71			1	3		4	4					1	13
72				5		2							7
73		2	1	1							1		5
74				4									4
75													0
76										1			1
77		5	4	9	5	2	2					2	29
78													0
79													0
80													0
81													0
82													0
83													0
84													0
85				13	10		1		5	1			30
86				10	5								15
87				6								1	7
88				12						1			13

89			17	10	6		3						36
90			9		2	1	2						14
91			8										8
92	1	3	9	2		2							17
Total	8	9	106	32	16	10	5	5	3	1	4		199

Table 17. Summary of wolf harvests in northwest Alaska during 1985-86 through 1991-92 by method of take according to sealing records (Alas. Dep. Fish and Game files).

Year	Hunting and trophy		Other[a]	Total
	Snowmachine assisted	Aircraft assisted		
1985-86	10	8	0	18
1986-87	12	22	0	34
1987-88	39	49	5	93
1988-89	80	11	2	93
1989-90	47	29[b]	4	80
1990-91	34	4	5	43
1991-92	46	6	4	56
Total	268	129	20	417
%	64.3	30.9	4.8	100

[a] Includes dog-team and unknown means.

[b] Twenty-seven known to be killed illegally and method of take unknown for 18, total harvest = 80.

Table 18. Summary by month and year of chronology of wolf harvests in northwest Alaska, 1985–86 through 1991–92 according to sealing records (Alas. Dep. Fish and Game files).

Month	1985–1986	1986–1987	1987–1988	1988–1989	1989–1990	1990–1991	1991–1992	Total	%
Sep	0	0	2	2	4	6	7	21	5.4
Oct	0	0	0	0	0	0	0	0	0
Nov	3	0	1	1	14	2	1	22	5.7
Dec	1	1	3	18	15	5	4	47	12.1
Jan	2	0	15	13	4	4	4	42	10.8
Feb	0	4	13	12	2	20	5	56	14.4
Mar	10	20	45	29	15	5	28	152	39.1
Apr	2	9	13	8	6		6	44	11.3
Unknown			1		2	1	1	5	1.3
Total	18	34	93	83	62[a]	43	56	389	100.1

[a] 80 reported harvested of which 27 taken illegally and date of kill unknown for 18.

Table 19. Sex ratios of harvested wolves in northwest Alaska, 1981-82 through 1991-92 according to sealing records (Alas. Dep. Fish and Game Files).

	Sex			
Year	M	F	Unrecorded	Total
81-82	10	8	0	18
82-83	25	19	1	45
83-84	30	14	3	47
84-85	42	21	0	63
85-86	9	6	0	15
86-87	23	10	1	34
87-88	52	33	8	93
88-89	42	36	5	83
89-90	27	25	28	80
90-91	17	15	7	39
91-92	29	23	4	56
Total	306	210	57	573
%	53.4	36.6	9.9	99.9

Table 20. Mean rates of population increase versus annual total and human-caused mortality rates of exploited wolf populations in North America (modified from Fuller 1989).[a]

Location	No. years	Annual finite rate of population increase	Exponential rate of population increase (r)	Annual mortality rate		Reference
				Total	Human-caused	
Northwest Alta.	2	0.40	-0.92	0.68[b,c]	0.68[b]	Bjorge and Gunson (1983)
Interior Alas.	4	0.69	-0.37	0.46[b,c]	0.46[b]	Gasaway et a l. (1983)
South-central Alas.	8	0.88	-0.13	0.45	0.36	Ballard et al. (1987)[d]
North-central Minn.	3	0.93	-0.08	0.31	0.31	Berg and Kuehn (1982)
Northwest Alas.	5	0.94	-0.06	0.63[e]	0.41[e]	This study
North-central Minn.	6	1.02	0.02	0.36	0.29	Fuller (1989)
Kenai Peninsula, Alas.	6	1.06	0.06	0.33	0.27	Peterson et al. (1984)[d]
Southwest Que.	4	1.11	0.10	0.36	0.19	Messier (1985a)[d]
Northwest Minn.	5	1.19	0.17	0.28	0.17	Fritts and Mech (1981)[d]
Northeast Alta.	2	1.21	0.19	0.15	0.15	Fuller and Keith (1980)[d]

[a] Correlation between exponential rate of increase and annual total mortality rate = weighted $r^s = -0.78$, 8df, $P < 0.010$. Correlation between r and annual human-caused mortality rate = weighted $r^s = -0.94$, df

= 8, $\underline{P} < 0.010$.

[b] Mortality rate of early winter population; assumes summer survival of ad = 1.00.

[c] Minimum mortality rate because only includes human-caused mortality.

[d] Recalculated.

[e/] Calculated using Heisey and Fuller (1985).

Table 21. Wolf kills (excludes scavenging) observed while monitoring radio-marked wolf packs in northwest Alaska, April 1987 through July 1992.

Months of obs.	Calf moose		Yearling moose		Adult moose	Unclassified moose	Calf caribou		Yearling caribou	
	No.	Age (mo.)	No.	Age (mo.)			No.	Age (mo.)	No.	Age (mo.)
May	2	0.1		12	1			0.1	2	12
Jun	2	1		13	1			1		13
Jul		2	1	14				2		14
Aug		3		15	1			3	1	15
Sep		4		16				4		16
Oct	1	5	2	17	2			5		17
Nov		6		18	1			6	2	18
Dec		7		19	1			7		19
Jan	1	8		20				8		20
Feb	1	9		21				9		21
Mar	4	10	1	22	15		1	10	1	22
Apr	6	11	4	23	20	4	2	11	3	23
Total	17		8		42	4	3		9	
%	10.1		4.8		25.0	2.4	1.8		5.4	

[a/] Includes both sexes.

Table 21. Continued.

Months of obs.	Adult caribou	Unclassified caribou	UnId.	Other	Total
May	3	1			9
Jun	1		1		5
Jul				1	2
Aug	3	1			6
Sep					0
Oct	5		2	3	15
Nov		1	1		5
Dec		1			2
Jan	4	2			7
Feb	1				2
Mar	12	1	1		36
Apr	35	2	3		79
Total	64	9	8	4	168
%	38.1	5.4	4.8	2.4	100.2

Table 22. Timing and species of prey scavenged by radio-marked wolf packs in northwest Alaska, April 1987 through July 1992.

Months of obs.	Calf moose		Yearling moose		Adult moose	Unclassified moose	Calf caribou		Yearling caribou	
	No.	Age (mo.)	No.	Age (mo.)			No.	Age (mo.)	No.	Age (mo.)
May		0.1		12				0.1		12
Jun		1		13	2			1	1	13
Jul		2		14				2		14
Aug		3		15				3		15
Sep		4		16				4		16
Oct		5		17				5		17
Nov		6		18				6		18
Dec		7		19				7		19
Jan		8		20				8		20
Feb		9		21				9		21
Mar		10		22	1			10		22
Apr		11		23		1		11	1	23
Total	0		0		3	1	0		2	
%	0		0		18.8	6.3	0		12.5	

Table 22. Continued.

Months of obs.	Adult Caribou[a]	Unclassified Caribou	UnId.	Other	Total
May	1				1
Jun	1				4
Jul					
Aug	1				1
Sep					
Oct					
Nov					
Dec					
Jan					
Feb					
Mar			3		4
Apr		1	3		6
Total	3	1	6	0	16
%	18.8	6.3	37.5	0	100.2

[a] Includes both sexes.

Table 23. Occurrence of radio-collared caribou from the Western Arctic Herd within or near the northwest Alaska wolf study area, winter and early spring 1988 through 1990.

		Within or near study area		Outside area	
Year	Date	No.	%	No.	%
1988	20 Jan	3	2.9	101	97.1
	03 Feb	1	1.0	103	99.0
	08 Feb	11	10.6	93	89.4
	16 Mar	47	45.2	57	54.8
	16-25 Apr	46	44.2	58	55.8
	Subtotal	108	20.8	412	79.2
1989	22 Feb	5	5.4	87	94.6
	11 Mar	0	0	92	100.0
	20 Mar	1	1.1	91	98.9
	22 Mar	5	5.4	87	94.6
	27 Mar	2	2.2	90	97.8
	30-31 Mar	6	6.5	86	93.5
	03-05 Apr	18	19.6	74	80.4
	Subtotal	37	5.7	607	94.3
1990	28 Jan	3	2.4	124	97.6
	19 Feb	0	0	127	100.0
	23 Mar	5	3.9	122	96.1
	06-09 Apr	4	3.1	123	96.9

19-20 Apr	6	4.7	121	95.3
Subtotal	18	2.8	617	97.2
Total	163	9.1	1636	90.9

Table 24. Dates monitored and number of prey killed and scavenged by 6 radio-marked wolf packs that were relocated and back-tracked daily in northwest Alaska, 1988 - 1990.

Year	Pack name	Traveling pack size[a]	Dates monitored	Caribou				
				Calf	Yearling	Ad F	Ad M	Ad Unk[b]
1988	Jade Mt.	1	31 Mar-21 Apr	0	1	0	0	0
	Purcell Mt.	9	1 Apr-28 Apr	0	0	4	2	2
	Rabbit Mt.	2	31 Mar-28 Apr	1	1	0	0	1
1989	Ingruk-sukruk	4	11 Mar-1 Apr	0	0	0	0	1
	Nuna Ck.	13	12 Mar-5 Apr	0	0	0	0	0
	Purcell Mt.	13	11 Mar-1 Apr	0	0	0	0	1
	Rabbit Mt.	2	11 Mar-5 Apr	0	0	0	0	0
1990	Dunes	5	21 Mar-27 Mar	0	0	0	0	0
	Dunes	5	6 Apr-22 Apr	0	0	0	0	0
	Ingruk-sukruk	4	8 Apr-20 Apr	0	2	0	0	1
	Nuna Ck.	23	23 Mar-27 Mar	0	0	0	0	0

	Nuna Ck.	19	5 Apr–19 Apr	0	0	0	0	1
	Purcell Mt.	11	6 Apr–20 Apr	1	0	1	1	7
Total		112		2	4	5	3	14
$\bar{x}$		8.5		0.15	0.31	0.38	0.23	1.08

Table 24. Continued.

Year	Pack Name	Traveling pack size[a]	Dates monitored	Moose					
				Calf	Yearling	Ad F	Ad M	Ad Unk[b]	Known scavenged species unk
1988	Jade Mt.	1	31 Mar–21 Apr	0	0	0	0	0	2
	Purcell Mt.	9	1 Apr–28 Apr	0	0	0	1	0	0
	Rabbit Mt.	2	31 Mar–28 Apr	0	0	0	0	0	2
1989	Ingruk-sukruk	4	11 Mar–1 Apr	0	0	0	1	3	3
	Nuna Creek	13	12 Mar–5 Apr	1	0	2	2	1	0
	Purcell Mt.	13	11 Mar–1 Apr	1	0	1	1	2	0
	Rabbit Mt.	2	11 Mar–5 Apr	0	0	1	1	0	0
1990	Dunes	5	21 Mar–27 Apr	1	0	0	0	1	0
	Dunes	5	6 Apr–22 Apr	2	0	0	0	3	0
	Ingruk-sukruk	4	8 Apr–20 Apr	0	0	0	0	0	0
	Nuna Creek	23	23 Mar–27 Mar	1	0	0	0	0	0
	Nuna Creek	19	5 Apr–19 Apr	1	0	0	0	4	0

	Purcell Mt.	11	6 Apr–20 Apr	1	0	0	0	1	0
Total		112		8	0	4	6	15	7
$\bar{x}$		8.5		0.62	0	0.31	0.46	1.15	0.54

[a] Messier (1985), Dale et al. (1993).

[b] Assumed to be ad females for all future calculations.

Table 25. Kgs consumed and kill rates (expressed as no. days/kill) for 6 radio-marked wolf packs that were relocated and back-tracked daily to previous locations during late winter and early spring in northwest Alaska, 1988-1990.

Year	Pack name	Pack Size		No. Days		Kgs prey[c]	Kg available/ wolf/day
		Traveling[a/]	Range	Monitored[b/]	Missed		
1988	Jade Mt.	1	1	21	0	80.8	3.8
	Purcell Mt.	9	1-11	27	2	900.4	3.7
	Rabbit Mt.	2	1-2	28	1	173.1	3.1
1989	Ingruksukruk	4	1-9	21	2	1340.4	16.0
	Nuna Creek	13	9-15	24	1	1693.5	5.4
	Purcell Mt.	13	9-14	21	0	1419.1	5.2
	Rabbit Mt.	2	1-2	25	1	640.5	12.8
1990	Dunes	5	1-5	6	1	412.5	13.8
	Dunes	5	2-5	16	3	1125.0	14.1
	Ingruksukruk	4	3-6	12	2	182.7	3.8
	Nuna Creek	23	23-24	6	0	112.5	0.8
	Nuna Creek	19	15-23	13	1	1378.3	5.6
	Purcell Mt.	11	5-13	14	1	1057.3	6.9
Total		111	72-132	234	16	10516.0	
$\bar{x}$		8.5	5.5-10.2	18.0	1.2	809.0	5.3

Table 25. Continued.

Year	Pack Name	Kg prey/Kg wolf/day[d]	Unadjusted days/kill days[e,f]	Adjusted days/kill[e,f]
1988	Jade Mt.	0.09	21.0	110.5
	Purcell Mt.	0.09	3.0	9.5
	Rabbit Mt.	0.07	9.3	53.8
1989	Ingruksukruk	0.37	4.2	4.8
	Nuna Creek	0.13	4.0	4.2
	Purcell Mt.	0.12	3.5	4.4
	Rabbit Mt.	0.30	12.5	11.7
1990	Dunes	0.32	3.0	4.3
	Dunes	0.33	3.2	4.3
	Ingruksukruk	0.09	4.0	20.0
	Nuna Creek	0.02	6.0	15.8
	Nuna Creek	0.13	2.2	2.8
	Purcell Mt.	0.16	1.2	5.1
Total				
$\bar{x}$		0.17	3.8	6.7

[a] Messier (1985), Dale et al. (1993).

[b] Excludes first day relocated.

[c] Assumes M, F, yearling, and calf caribou wt 96, 76, 67, and 36 kg (J. Davis, Alas. Dep. Fish and Game,

Fairbanks, pers. comm.) respectively, with % consumable equal to 85, 87, 87, and 95% (Sumanik 1987), respectively. Yearling caribou wt was estimated from relationship of calf caribou to calf and yearling moose. Adult M, adult F, yearlings, and calf moose were assumed to weigh 454, 400, 278, and 150 kg respectively (Franzmann et al. 1978, Hayes et al. 1991) and that 75% was consumable (Peterson 1977, Ballard et al. 1987, Sumanik 1987). We assumed scavenged carcasses had 15kg of prey available and that 75% were consumed.

[d] Used mean mass of all captured wolves.

[e] Calculated by assigning prey the following values based upon adult female moose equality 1.0: adult bull moose = 1.14, adult female moose = 1.00, yearling moose = 0.70, calf moose = 0.38, adult bull caribou = 0.27, adult female caribou = 0.22, yearling caribou = 0.19, and calf caribou = 0.11.

[f] Excludes scavenged kills.

Table 26. Ungulate biomass index/wolf versus estimated winter consumption rates of ungulates by wolves during winter in North America (modified from Fuller 1989).

Location	Major prey species	Ungulate biomass index/ wolf	Consumption rate in winter		Reference
			kg/wolf/ day	kg/kg of wolf/day[a]	
East-central Ont.	Deer	112	2.9	0.10 (30)	Kolenosky (1972)
Northern Alta.	Bison	152	5.3	0.14 (38)	Oosenbrug and Carbyn (1982)
West-central Yuk.	Sheep	153	3.0	0.08 (37)	Sumanik (1987)
North-central Minn.	Deer	161	2.0	0.06 (34)	Fuller (1989)
Southwest Que.	Moose	162	2.2	0.07 (30)	Messier and Crete (1985)
Northeast Minn.	Deer	178	2.9	0.10 (30)	Mech (1977)
Isle Royale, Mich.	Moose	225	7.2	0.22 (33)	Peterson (1977)
Northeast Alta.	Moose	231	5.5	0.14 (38)	Fuller and Keith (1980)
Isle Royale, Mich.	Moose	264	4.9	0.15 (33)	Peterson and Page (1988)
Northwest Alas.	Caribou-moose	267	5.3	0.17 (43)	This study
Denali Park, Alas.	Moose	334	4.5	0.11 (40)	Haber (1977)
Southwest Manit.	Elk	336	6.8	0.21 (32)	Carbyn (1983)
Kenai Peninsula, Alas.	Moose	345	4.8	0.12 (40)	Peterson et al. (1984)
Northwest Minn.	Deer	400	2.9	0.09 (32)	Fritts and Mech (1981)

South-central	Alas.	Moose	659	7.1	0.18 (40)	Ballard et al. (1987)

[a]Estimated mean mass (kg) of wolf in each area.

Table 27. Average number of days (n) spent at ungulate kills by 6 radio-marked wolf packs during late winter and early spring in northwest Alaska, 1988–1990[a].

	Pack		After moose kill				
Year	Name	Size	Calf	Yrl.	Ad F	Ad M	2 Ad's.
1988	Jade Mt.	1					
	Purcell Mt.	9				1 (1)	
	Rabbit Mt.	2					
1989	Ingruksukruk	4			1.7(3)		
	Nuna Creek	13			1.7(3)	1.5(2)	
	Purcell Mt.	13			2.5(2)	2 (1)	
	Rabbit Mt.	2			9 (1)	3 (1)	
1990	Dunes	5	1(1)		1 (1)		
	Dunes	5	1(1)	1(1)	1 (1)		2(1)
	Ingruksukruk	4					
	Nuna Creek	19	1(1)		1.3(4)		
	Purcell Mt.	11			1 (1)		
Weighted $\bar{x}$		7.3 (12)	1(3)	1(1)	2 (16)	1.8(5)	2(1)

Table 27. Continued.

Year	Name	Pack		After caribou kill				
		Size	Calf	Yearling	AdF	AdM	ADF and Calf	7Ad's
1988	Jade Mt.	1		1(1)				
	Purcell Mt.	9			1.2(6)	1.5(2)		
	Rabbit Mt.	2	1(1)	1(1)	1 (1)			
1989	Ingruksukruk	4			1 (1)			
	Nuna Creek	13						
	Purcell Mt.	13			1 (2)			
	Rabbit Mt.	2						
1990	Dunes	5						
	Dunes	5						
	Ingruksukruk	4		1(1)	1 (1)			
	Nuna Creek	19			1 (1)			
	Purcell Mt.	11				2 (1)	1(1)	1(1)
Weighted $\bar{x}$		7.3 (12)	1(1)	1(3)	1.1(12)	1.7(3)	1(1)	1(1)

[a] Assumes unclassified moose and caribou were adult females.

Table 28. Time interval in days (n) between ungulate kills for 6 radio-marked wolf packs in northwest Alaska during late winter and early spring, 1988-1990[a].

Year	Pack Name	Size	After moose kill				
			Calf	Yrl.	Ad F	Ad M	2 Ads.
1988	Jade Mt.	1					
	Purcell Mt.	9				2 (1)	
	Rabbit Mt.	2					
1989	Ingruksukruk	4			5.3(1)		
	Nuna Creek	13			6.3(3)	2.5(2)	
	Purcell Mt.	13			4.7(3)	3 (1)	
	Rabbit Mt.	2				6 (1)	
1990	Dunes	5			3 (1)		
	Dunes	5	4 (1)	3(1)	3 (1)		3(1)
	Ingruksukruk	4					
	Nuna Creek	19	3 (1)		2 (4)		
	Purcell Mt.	11			3 (1)		
Weighted $\bar{x}$		7.3 (12)	3.5(2)	3(1)	4.1(16)	3.2(5)	3(1)

Table 28. Continued.

Year	Pack Name	After caribou kill					
		Calf	Yearling	Ad F	Ad M	Ad F and Calf	7 Ads
1988	Jade Mt.		2(1)				
	Purcell Mt.			1.8(6)	6 (1)		
	Rabbit Mt.		6(1)	1 (1)			
1989	Ingruksukruk			3 (1)			
	Nuna Creek						
	Purcell Mt.			1 (1)			
	Rabbit Mt.						
1990	Dunes						
	Dunes						
	Ingruksukruk		7(1)	2 (1)			
	Nuna Creek						
	Purcell Mt.				5 (1)	1(1)	3(1)
Weighted $\bar{x}$		1(1)	5(3)	2.8(10)	5.5(2)	1(1)	3(1)

[a] Assumes unclassified moose and caribou were adult females.

Table 29. Marrow fat levels of various bones of wolf-killed caribou and moose from northwest Alaska, 1989 and 1990.

Species & date collected	Sex	Age (yrs)	Ramus	Meta-carpus	Meta-tarsus	Tibia	Fibia	Radius	Hum-erus	Femur
Caribou										
14 Apr 89	F	11.8			74		76			66.6[a]
09 Apr 89	F	8.8					83			83
Apr 90	Unk	Ad		95.2	90.2	84.3				95.8
					90.3	92				
Apr 90	F	5.8		66.3				70.3	59.8	63.6[a]
								60.8		
25 Mar 90	F	Ad			84.8			82.5	92.9	96.7[a]
08 Apr 90	F	8.8			76.3					89.4
15 Apr 90	M	7.8			88.2	94.7			94.3	95.4
					88.2				90.2	96.9
08 Apr 90	F	5.8			90.4	88.9				88.8
18 Apr 90	F	4.8		88.9						90.7
				88.8						
04 Mar 90	Unk	7.8			85.3	13.4				91.6
04 Mar 90	Unk	9.8		74.1				75.8		63.5
30 Apr 90	Unk	9.8						22	43	26
	$\underline{n}$	10		5	9	5	2	5	5	12
	$\bar{x}$	8.1		82.7	85.3	74.7	79.5	62.3	76	79.4[b]

	SD	2.05		10.7	5.8	30.8	3.5	21.4	20.8	20.1
Moose										
26 Mar 90	Unk	0.8		21.4		44.1				15.8
12 Apr 90	Unk	0.8		86.5				82.2	90	93.8[a]
	n	2		2		1		1	1	2
	$\bar{x}$	0.8		54		44.1		82.2	90	54.8
	SD	0		32.6		0		0	0	39
14 Mar 89	Unk	1.8	52.9	89				59		61.9[c]
			55.7							65[c]
01 Apr 89	F	11.8	61.7		6		7			67.3[c]
										6
										6
14 Apr 89	F	1.8	48.2		57		50			56.8[c]
										49
23 Mar 90	Unk	Ad		90.4	82.7	82.7		88.5		
04 Apr 90	Unk	15.9	58.7							76.3
04 Apr 90	F	3.8	63.9	92				77		73.9[c]
	n	5	6	3	3	1		2	3	6
	$\bar{x}$	7	56.9	90.5	48.6	82.7		28.5	74.8	64.3[b]

	SD	5.8	5.3	1.21	31.9	0		21.5	12.1	8.8[b]
02 Apr 89	M	1.8	18.9	45	39		30	31	23	24.9[c]
			16.1		39		31			21.8[c]
19 Apr 89	M	11.8	22.8							29.1[c]
			24.7							31.2[c]
	n	2	4	1	2		2	1	1	2
	$\bar{x}$	6.8	20.6	45	39		30.5	31	23	28.6[b]
	SD	5	3.3	0	0		0.5	0	0	3.7[b]

[a] Estimated from equations provided by Davis et al. (1877) using most proximal longbone.

[b] When >1 sample available the highest value was used.

[c] Estimated from equations provided by Ballard et al. (1981) using the ramus.

Table 30. Comparison of average longbone marrow fat %(n) during late winter for moose and caribou by cause of death from several study areas in North America.

Species-Age	Location	Cause of death			Source
		Starvation	Wolf-killed	Accidental	
Moose-calf	Kenai Peninsula, Alas.	7.3 (86)	22.1 (8)	28.3 (21)	Franzmann and Arneson (1976)
	South-central Alas.	12 (20)	31 (49)	24 (8)	Ballard et al. (1987)
	Yukon Territory		60 (17)		Hayes et al. (1991)
	Denali Nat Park, Alas.		32-67[a] (19)		Mech et al. (1993)
	Northwest Alas.		54.8 (2)		This study
Moose-adult	Kenai Peninsula, Alas.	7.3 (11)	69.9 (11)	69.2 (44)	Franzmann and Arneson (1976)
	South-central Alas.	52 (10)	77 (106)	79 (13)	Ballard et al. (1987)
	Yukon Territory		80 (32)		Hayes et al. (1991)
	Denali Natl. Park, Alas.		62-74[b] (26)		Mech et al. (1993)
	Northwest Alas.		64.3[c/] (6)		This study
Caribou-calf	Northwest Alas.	8 (7)	50 (2)	70 (6)	Davis and Valkenburg (1985)
	Denali Natl. Park, Alas.		31-45[a] (14)		Mech et al. (1993)
Caribou-adult	South-central Alas.		81 (21)		Ballard et al. (1987)

Northwest Alas.	5.3[c]	(7)	60[c] (15)	51[c] (18)	Davis and Valkenburg (1985)
Denali Natl. Park, Alas.			62–86[b] (33)		Mech et al. (1987)
Northwest Alas.			80.6 (13)		This study

[a] February through April.

[b] Adult Females, February through April.

[c] Adult females.

CHAPTER 2

USE OF LINE-INTERCEPT TRACK SAMPLING FOR ESTIMATING WOLF DENSITIES

Abstract: During spring 1990 and spring 1991 we tested the use of line-intercept sampling of tracks for estimating wolf (Canis lupus) densities for a known wolf population occupying a 6464 km^2 study area in northwest Alaska, and for a population estimated by traditional aerial reconnaissance in a 5011 km^2 survey area in interior Alaska. In each study area we used 7 randomly chosen samples, each consisting of 5 systematically spaced transects. Based upon telemetry studies the minimum number of wolves known to occupy the northwest Alaska study area was 48. The population estimate based upon line-intercept sampling was 50.7 (80% CI = 33.4 to 67.9). The biological confidence interval was 43 to 68.

The estimated numbers of wolves occupying the interior survey area, based upon aerial reconnaissance surveys, was 36. The population estimate based upon line-intercept sampling was 33.4 (80% CI = 23.3 to 43.6). The biological confidence interval was 25 to 44. Advantages of the line-intercept procedure over other survey methods include objectivity, repeatability, speed, reduced cost, reasonable accuracy, and measurable precision.

Obtaining accurate and precise estimates of wolf (Canis lupus) population density is costly and time consuming because of relatively low density and secretive behavior of the species. Since the early 1970's a number of state, provincial, and federal governments have attempted to monitor the status of wolf populations regularly. Methods included harvest statistics (Rausch 1967), howling surveys (Harrington and Mech 1982), hunter observations to assess trend (Crete and Messier 1987), a variety of aerial reconnaissance surveys (Stephenson 1978, Gasaway et al. 1983, Crete and Messier 1987), and radio telemetry studies (Ballard et al. 1987, Fuller and Snow 1988a). A number of problems exist with each method.

Howling surveys are time consuming, expensive, require road access, limited to relatively small areas, and imprecise (Crete and Messier 1987, Fuller and Sampson 1988b). Estimates obtained from hunter observations are also relatively imprecise and require a large sample of hunters (Crete and Messier 1987); a large hunter sample is not practical for many areas of North America. Aerial track counts using transects were evaluated and found unsatisfactory by Crete and Messier (1987).

Aerial reconnaissance surveys (Stephenson 1978, Gasaway et al. 1983) are widely used in western Canada and Alaska for assessing wolf densities. This method differs

considerably from the aerial track counts evaluated by Crete and Messier (1987); smaller and slower aircraft are used, pilots and observers are experienced wolf trackers, and transects are flown only in homogeneous habitats. Varying intensity searches are conducted of habitats frequented by wolves (e.g., ridges, shorelines, and streams). When wolf tracks are encountered they are followed until wolves are observed and the number and color composition of the pack are determined. Pack size is estimated from tracks if wolves are not observed. Tracks, wolves observed, and prior knowledge of wolf pack locations are used to form a mosaic of wolf pack areas. Numbers of wolves in each area are estimated from the survey data resulting in best, low, and high estimates that are not estimates of precision. This method appears to work well in Alaska with resident wolf packs, but may not in areas where portions or all of the wolf population is migratory and/or wolves exist in relatively low densities. The method was evaluated on a cursory basis by Stephenson (1978), who determined that in one area the method provided a good estimation (within 80-96%) of wolf density in relation to what was estimated from radio-telemetry studies. W. B. Ballard (Alas. Dep. Fish and Game, unpubl. data) had similar results with a test of a pilot-observer team that was "current" (<5 years since last wolf survey) at wolf tracking. However,

results were 50% lower with a pilot-observer team that was experienced but not current (>5 years since last wolf survey).

To date, the best method for estimating wolf population density involves use of radiotelemetry to estimate pack territories and sizes, and the numbers of wolves in each pack. While the resulting density estimates are accurate and repeatable (Fuller and Snow 1988a), they are also expensive and time consuming to obtain, and do not contain measures of precision. High cost makes this method impractical for routine management.

A cost effective and practical method of surveying wolves over large geographic areas would ideally be accurate and have a high degree of precision. Becker (1991) reported a method for estimating lynx (Felis lynx) and wolverine (Gulo gulo) densities in Alaska using a line-intercept track sampling method that we have termed the track intercept probability estimator (TIP survey). The greatest potential advantage for use of TIPS on wolves is that it provides a measure of precision not previously available. The TIPS method has been used for surveying wolves (Becker and Gardner 1990, Gardner and Becker 1991), but its' accuracy and precision within a known population of wolves has not been assessed, nor have the results been compared with those from traditional aerial reconnaissance surveys. This study

compares TIP survey (Becker 1991) estimates to a radiotelemetry based estimate (Kobuk study area) and to an estimate based upon aerial reconnaissance surveys (Minto study area). We discuss advantages and disadvantages in relation to other available survey methods.

STUDY AREA AND METHODS

The Kobuk study area included the winter range of the western Arctic caribou (Rangifer tarandus) herd and portions of Kobuk Valley National Park, Selawik National Wildlife Refuge, and Koyukuk National Wildlife Refuge in northwest Alaska. Within the 12 279 km^2 wolf study area (Ballard et al. 1990), we selected a 6464 km^2 TIP survey area (Fig. 1) where radio contact had been maintained with 3 wolf packs during the previous 3 years. Two additional packs without collared members (uncollared packs) were observed within the TIP survey area before the survey, and their numbers were determined by direct count prior to the survey. Territory boundaries of instrumented packs were estimated using outermost radio-relocations (Mohr 1947). Territories of uncollared packs were estimated based upon their spatial relationship to collared packs, wolf sightings, and mapped travel routes observed during capture and monitoring flights.

During spring 1991 we conducted aerial reconnaissance surveys (Stephenson 1978) in the Minto study area to determine wolf densities (Fig. 2). Surveys were conducted during clear weather, 1-5 days following fresh snowfalls $\geq$75 mm. One to 3 aircraft (Piper Supercub or Bellanca Scout) searched 1000 - 2500 km^2 search blocks on each of 5 survey days. We resurveyed search blocks on different days and

concentrated search efforts on probable wolf travel routes. Once encountered, wolf tracks were followed until wolves were sighted or pack size could be estimated from tracks. We backtracked wolves until tracks appeared old and plotted all track segments on 1:250 000 scale U.S.Geologic Survey maps.

The aerial reconnaissance estimate of wolf numbers included wolves observed plus track estimates. Individual packs were identified by size and color composition. Relative timing of track observations, hunter and trapper sightings, and repetitive surveys of search blocks helped differentiate between observed packs and those estimated from tracks. No correction factor was applied for single wolves because we had no basis for estimating the number of single wolves.

Before completing the aerial reconnaissance survey we conducted a TIP survey within a 5011 km^2 portion of the Minto study area to provide an alternate estimate of wolf numbers and to compare the TIP survey estimate with that obtained from the aerial reconnaissance survey.

For both study sites the TIP survey areas were designed as rectangles and positioned on a 1:250 000 scale map so that randomly selected transects would have a high probability of crossing wolf travel routes (e.g., ridges and streams). Locations of surveyed transects were selected

using a randomly repeated systematic sample design (Becker 1991). Each sample unit consisted of 5 systematically spaced transects that were 38.6 km long in the Kobuk study area and 24.6 km long in the Minto study area. A random sample of 7 of these sample units was selected by randomly choosing the starting point on the x-axis for the first transect in each systematic sample. The randomization was restricted by forcing a minimum spacing of 1.6 km between any 2 adjacent transects. Other combinations of numbers of samples and transects can be used, but previous experience indicated that 7 samples composed of 5 transects was a desirable sampling scheme (Gardner and Becker 1991). We calculated 80% confidence intervals (CI) for each estimate. We chose 80% CIs to prevent making a Type II error of falsely concluding that there was no change in the population.

General procedures for conducting the survey were described by Becker (1991), Becker and Gardner (1990), and Gardner and Becker (1991). The mathematical equations, sampling theory, and model assumptions are detailed in Becker (1991). Becker (1991) outlined 4 assumptions necessary when line-intercept track surveys are conducted from fixed wing aircraft: (1) all wolves in the study area move and deposit tracks prior to the survey; (2) all wolf tracks that cross a transect are detectable and

identifiable; (3) tracks encountered can be followed to the wolf's present location and backtracked to where it had bedded-down during the snow storm or where the tracks can be classified as "old"; and (4) the distance wolves traveled parallel to the x-axis since the last snow storm can be determined by tracking. Field procedures were designed to ensure compliance with these assumptions and to verify their validity.

Each survey aircraft (Piper Supercubs and Bellanca Scout) was assigned 7 transects. Transects were initiated from the western boundary of both study areas. Following completion of all assigned transects, each aircraft flew irregular searches (herein referred to as renegade searches) between transect lines to check if any wolf tracks had been missed. Survey aircraft maintained airspeeds of approximately 90-130 km/hour at altitudes of 60-160 m.

Before and after the survey in the Kobuk study, a separate aircraft (Piper Supercub that did not participate in the survey) located, by use of radiotelemetry, and backtracked all radio-collared wolves associated with the study. This procedure allowed us to determine if all radio-collared wolves were in the study area and were available for counting. It also provided an opportunity to determine if the survey aircraft could locate, backtrack, and estimate pack sizes for packs of known numbers.

Topography of the survey area ranged from flat (30 m) along the Kobuk River and along the southern boundary of the area to the gently sloping north or south facing slopes from the crest (536 m) of the Waring Mountains. North of the Kobuk River, which runs through the area from east to west, several steep ridges (1100 m) run from north to south.

Vegetation of the area ranged from thick black (Picea merino) and white (P. glauca) spruce forests along the Kobuk River and its major tributaries, grading into sparser stands of spruce and mixed shrub consisting of willow (Salix spp.), alder (Alnus spp.), and birch (Betula glandulosa, B. nana, and B. papyrifera). Higher elevations were dominated by mat-cushion and upland tundra and bare rock.

The area has a maritime climate during snow-free periods. Winter and summer temperatures average -11.5° and 9.4°C, respectively. The area is often snow-covered from October through May. Annual precipitation averages 680 mm; half of which occurs during July and August.

The Minto study area ranges in elevation from 90 to 1400 m. The southern portion of the study area is characterized by flat terrain with numerous lowland lakes interspersed with mixed birch, both black and white spruce, and wet marshlands. North of Minto Flats, the terrain rises through rolling, forest covered hills to a prominent east-

west alpine tundra ridge along the northern boundary of the area. Drainages flow south into the Tanana River.

Climate of the area is continental. Annual precipitation averages 310 mm, half of which occurs during June, July, and August. Accumulated snow depths average 480 mm on 1 March and average daily temperatures range from 15.3 °C in July to -21.8 °C in January

RESULTS

Kobuk Study Area

A snow storm from 26 to 28 April 1990 brought 48 mm of fresh snow to the study area. Sixty-four cm were already on the ground at the time of the storm. An earlier storm from 21-23 April resulted in 310 mm of fresh snow, so survey conditions were excellent on 1 May. On 1 May 1990, approximately 3 days after the storm, 5 fixed-wing aircraft flew 7 systematic samples consisting of 5 38.6-km long transects (Fig. 3). We expended 36.6 hours flying transects and renegade searches. During the approximate 5 to 7.5 hours of renegade searches, 4 of 5 aircraft found no additional wolf sign. One aircraft missed a pack of 3 wolves (Waring Mountain pack) that had crossed the southern-most transect on 2 occasions.

Forty-eight wolves were accounted for during the survey (Table 1): 43 wolves observed and tracks of 5 others recorded. All 5 packs known to occur within the study area were located.

All wolves encountered were successfully tracked and backtracked. However, there were discrepancies between pack size estimates during the survey and those obtained before and after the survey. For example, the radio-tracking aircraft could only account for 10 wolves in packs from the Salmon River and middle Kobuk River, but the survey crew

counted 11 in each. The Dunes Pack contained 5 individuals and had been observed daily during the preceding 2 week period. The survey crew (based upon track counts) estimated it to contain 6-7 wolves. The Nuna Creek Pack numbered 18 wolves the morning before the survey but during and after the survey only 16 wolves were counted in the pack. Sometime during the survey, 2 radio-collared wolves left their pack and died. They were missed during the survey. Subsequent observations revealed that a rabies enzootic was in progress (Brand et al., this volume). Although no single or "lone" wolves were radio-collared, losses from some instrumented packs over the 3-week period prior to the survey (Nuna Creek pack originally had numbered 21 individuals) suggested some single wolves were either in the area, had been killed by local hunters, or died of rabies.

Wolves were encountered on all 7 of the systematic samples (Table 1). Average group size was 8 $\pm$ 5.6 (SD). Average distance moved perpendicular to the transects since the last snow storm was 18.9 $\pm$ 9.3 (SD) km per wolf group. The resulting wolf population estimate based upon the transects was 50.7 with an 80% confidence interval (CI) of 33.4 to 67.9 (Table 1). The density estimate was 7.8 wolves/1000 km^2 (80% CI = 5.2-10.5 wolves/1000 km^2).

Minto Study Area

We flew 50.5 hours of aerial reconnaissance surveys in the Minto study area between 12 March and 2 April 1991. The best estimate was 64 wolves (7.2 wolves/1000 km^2) in 14 packs within the 8840 km^2 study area (Table 2). We calculated low and high estimates of 58 and 71 wolves, respectively by excluding or including packs whose separate identities could not be clearly established. Among the 14 packs included in the best estimate, pack sizes ranged from 2 to 12 wolves per pack and averaged 4.6.

Deriving estimates from aerial reconnaissance surveys requires subjective decisions because complete home ranges are not known and estimates are often based upon tracks rather than observed wolves. Searching the survey area repeatedly after consecutive snowfall events helped us differentiate between adjacent packs because we gained additional wolf movement information after each fresh snowfall. For example, during aerial reconnaissance searches on 21 March, 3 days following a 75 mm snowfall, we encountered wolf tracks in the northeastern corner of the study area. These tracks led us 90 km along an open ridge to the northwestern corner of the study area. Two aircraft encountered the track segment and although only 6 wolves were sighted, each search team independently estimated 10-14 wolves from tracks. Later, on 1 and 2 April, after fresh

snowfall covered the tracks observed on 21 March, we saw 3 packs containing 19 wolves in the vicinity of the track segment observed on 21 March.

Resurveying the study area following consecutive snowfalls enhanced our abilities to estimate wolf numbers based on aerial reconnaissance surveys. However, under real-life conditions limited money for aerial reconnaissance surveys or weather often preclude survey efforts. When these limitations are encountered subjective decisions enter into the final estimate. In this case, of the 58 wolves estimated in the low estimate, only 39 wolves were actually observed hence, the minimum estimate could be construed to be 39 wolves (4.4 wolves/1000 km^2).

On 31 March, 2 days after a large storm ended (580 mm of new snow), we flew a TIP survey within a 5011 km^2 rectangle within the Minto Study Area (Fig. 4). Three aircraft (2 supercubs and 1 Bellanca Scout) flew 7 systematic samples consisting of 5 24.6-km transects. We flew 19.5 hours to complete transects and to conduct renegade searches between transects. The entire TIP survey area had been subjected to aerial reconnaissance surveys on 20 and 21 March, but all tracks observed during those surveys had been covered by snow between 24 and 29 March.

During the TIP survey, we encountered tracks of 4 wolf packs totalling 25 wolves. We successfully tracked 3 packs

until wolves were sighted. The fourth pack (2 wolves) was tracked to where the wolves were concealed by thick spruce. A fifth pack (Allen Creek Pack) was found between transects during the renegade search, but that pack had moved only a short perpendicular distance and failed to cross survey transects. The following day, during aerial reconnaissance surveys, a sixth pack (Hutlinana Creek Pack) was successfully tracked within the TIP survey area. Again, the entire track segment lay within the TIP survey area, but had not crossed any of the survey transects. Therefore, we did not detect 2 wolf packs totalling 13 wolves during the TIP survey. Because those packs did not cross survey transects, they did not enter into calculations of the TIP wolf population estimate. We continued aerial reconnaissance surveys through 2 April, but found no additional packs.

Wolves were encountered on all 7 systematic samples within the Minto TIP survey area (Table 3). Average group size was 6.3 $\pm$ 4.2(SD) and average distance moved perpendicular to the transects since last snowfall averaged 13.1 $\pm$ 5.7 (SD) km per group. The TIP wolf population estimate within the 5011 km^2 survey area was 33.4 with an 80% confidence interval (CI) of 23.3 to 43.6 (Table 3). The density estimate was 6.7 wolves/1000 km^2 (80% CI = 4.6 - 8.7 wolves/1000 km^2). In comparison, the best estimate from the aerial reconnaissance survey for the TIP survey area (5011

km^2) was 36 wolves, and the density estimate for the entire Minto study area (8840 km^2) from aerial reconnaissance surveys was 7.2 wolves/1000 km^2. Therefore, similar wolf population and density estimates were obtained from the aerial reconnaissance and TIP surveys.

DISCUSSION

The TIP survey method is objective and repeatable, and appears to alleviate the problem of dealing with the proportion of lone wolves in the population estimate (Fuller and Snow 1988a). Other methods rely on estimates from the literature or costly radiotelemetry studies. With the line-intercept method, the proportion of lone wolves included within the estimate is determined by actual survey data.

The maximum size of a survey area for application of the TIP survey method is limited primarily by the number of aircraft and available flight time per aircraft. Factors which affect how aircraft are utilized include: (1) numbers and lengths of transects to be surveyed; (2) target animal densities and movement rates and patterns since last snowfall, which influence time necessary for forward and backtracking; and (3) commute times between aircraft facilities and the study area, ferry times between transects, and the availability of cached fuel in or near the study area. Because the survey method is dependent upon the distance moved by target animals perpendicular to the transects, surveying the entire area quickly is important. While all tracks of target animals intercepting a transect must be detected and tracked, all target animals in the

survey area need not be detected by having their tracks intercept a transect.

The size of our study areas (6464 km^2 and 5011 km^2) was limited by available aircraft, logistics, and in the Kobuk study by the desire to evaluate the assumption of track detectability, which required a high probability that tracks made by instrumented packs would be intercepted by >1 transect. The aircraft were assigned 270 km and 287 km of transects to search and averaged 7.3 hours and 6.5 hours of survey effort (not including ferry time) in the Kobuk and Minto Study Areas, respectively. Each aircraft was allocated approximately 2 hours of commute time, about 6 to 6.5 hours to fly the transects and follow intercepted tracks, and about 0.5 to 1 hour for renegade searches. Because of the potential for pilot fatigue, maximum flight time per survey day should not exceed 8.0 hours. Study areas ranging from 4,556 to 10,343 km^2 have been surveyed with this method (Becker and Gardner 1990; Gardner and Becker 1991; G. Carroll, Alas. Dep. of Fish and Game, unpublished data; this study). The study areas could have been doubled in size with modest increases in commute time. However, doubling would have required less intensive sampling (fewer transects or fewer samples), less time per aircraft for renegade searches, and probably would have resulted in decreased precision. The sampling intensity we

used provided increased precision because most packs crossed several transects, therefore data from most packs were included in more than one systematic sample.

The survey method has a number of potential problems, most of which are common to all aerial survey techniques. Spotting wolf tracks in the snow from aircraft and then tracking and backtracking requires a higher level of pilot expertise than required for most other wildlife surveys. Use of inexperienced pilots would undoubtedly result in underestimates of wolf population sizes. Although experienced observers are helpful, most of the spotting and tracking depends upon the pilot.

Based upon computer simulations, Gardner and Becker (1991) recommended conducting TIP surveys 4-5 days following a snow storm. That recommendation assumed a snowfall >70 mm and relatively low caribou densities. Our surveys were conducted on the second or third days following a snow storm and accurately estimated the numbers of wolves relative to known or estimated numbers inhabiting the area. More research is necessary to determine the optimum time after snow storms for conducting TIP surveys on wolves.

Lack of population closure (i.e., failure of all wolves whose home ranges overlap the study area, to be within the study area during the survey) may also affect density estimates derived from aerial reconnaissance or general

line-intercept surveys. The aerial reconnaissance survey method can greatly overestimate wolf densities when wolves are observed in the area, but only a small portion of their home range occurs there. In one instance, one wolf pack that had <10% of its territory within the count area was included in the estimate (W. B. Ballard and J. S. Whitman, Alas. Dep. of Fish and Game, unpubl. data). The result was that the population was overestimated by 16% in a 8671 km^2 area by the aerial reconnaissance method.

Becker (1991) suggested that during TIP surveys, intercepted tracks be completely tracked forwards and backwards, so the distance wolves travelled parallel to the x-axis could be accurately mapped. If ≥50% of that distance was travelled within the study area, the data for that pack would be included in wolf estimate calculations. An alternative method would be to include only data from wolves that were in the study area during the aerial survey. If wolves made tracks in the study area but then left prior to the survey, data from those packs would not be considered. The latter method would provide a better estimate of wolves in the study area on the day the survey was flown, but it could yield extreme, imprecise estimates when a wolf pack was found shortly after it had entered the study area. We recommend using Becker's closure rule because it would tend to provide a better-behaved precision estimate and a better

overall seasonal estimate of wolf density. During our surveys, we used Becker's (1991) recommendations in those instances when wolves were tracked outside the study area (Figures 3 and 4). Closure rules are necessary to prevent biased wolf density estimates.

Gardner and Becker (1991) reported an "ongoing wolf-hunting season" affected use of the method in their study area. Apparently wolf packs had been hunted (aircraft assisted) immediately before the counts were initiated, and packs and individual pack members were scattered over large areas. Hunting regulations over most of Alaska until recently allowed hunters to use aircraft to spot wolves but required them to land to shoot. The Alaska Board of Game made this practice illegal in many areas of the state beginning 1 July 1992, consequently, this factor should be less important in future surveys.

Tracking wolves through dense forest from fixed-wing aircraft is difficult, time consuming, and requires good snow conditions. Becker and Gardner (1990) suggested accurate counts would not be expected in large areas with low sightability, such as those with dense forests. If sightability was low, the assumption that all tracks could be detected and followed would probably be violated. Although our Kobuk study area contained thick stands of spruce along riparian areas, it is probably representative

of ideal survey conditions because dense vegetation only occurs in relatively narrow strips. In contrast, our Minto study area contained large forested areas. We did not fail to detect wolf tracks in the forested habitats, based on renegade searches and on subsequent aerial reconnaissance surveys. Yet, more testing, using radio collared wolves, is needed to evaluate sightability in closed habitats under varying conditions of light, snow and wolf densities.

Wolf packs stay close to ungulate kills for 2-5 day periods (Ballard et al. 1987) and for as long as 8 - 15 days (Messier 1985, Ballard et al. 1987). Consequently, some packs may not move between the last snow storm and the time the survey is conducted. The encounter of these packs could cause the point estimate of population size to be unreasonably high and of low precision. For example, if the Allen Creek pack of 7 wolves (Minto survey area) had crossed a transect after traveling a perpendicular distance of only 1.0 km, the estimate would have been 72.8 wolves rather than 33.4, and the 80% Confidence Interval would have been $\pm$ 64% of the estimate rather than $\pm$ 30% of the estimate. Lengthening the period between end of snowfall and initiation of the survey will decrease the chance of encountering such situations. A similar situation as discussed above was probably the cause of inflated population estimates made by Becker and Gardner (1990).

Our original intent was to develop a wolf census method for use on the wintering grounds of the western Arctic caribou herd. Because the TIP method is highly dependent on good wolf tracking conditions, it cannot be used in areas of high ungulate density, particularly on caribou winter range. No accurate and precise methods currently exist for surveying wolves on caribou winter range, other than costly radiotelemetry studies. Although no caribou were present in our Minto study area and only small, scattered groups were encountered in our Kobuk study area, large numbers would greatly complicate survey attempts.

In spite of this problem with resident ungulates, the TIP method contains a measure of precision not obtained with other aerial survey methods. Equally important, the method is objective, repeatable, fast, and appears to provide reasonably accurate population estimates. Unlike aerial reconnaissance surveys, investigators are not required to distinguish between different wolf packs, or to detect all wolf packs within the survey area. On the negative side, statistical precision obtained with the method is low. The biological precision (number observed and the upper 80% limit) however, is a large improvement over other wolf-survey methods. We hope to further improve precision by experimenting with different transect orientation designs and by more closely defining optimum survey periods

following snowfall.

The TIP method is relatively inexpensive compared to telemetry studies. Total costs for such surveys ($135/hour/aircraft) exclusive of manpower ranged from $1,900-$2,600 (U.S. dollars) in south-central Alaska (Gardner and Becker 1991) to $3,250 in the Minto Study area and $11,100 in the Kobuk Study Area. The Kobuk study costs represented an extreme because of difficult logistics which required us to use aircraft and personnel from outside areas. The actual Kobuk survey cost was $4,758, the remainder being transportation costs. Gardner and Becker's (1991) costs represent the low end because experienced pilots and observers were located close to the study areas and commute times were minimal.

Accurate and precise density estimates may allow extrapolation of survey results to larger areas of management significance. Simple extrapolations to obtain population estimates may be appropriate if study area boundaries contain representative proportions of habitat for the larger area of interest. Extrapolation may otherwise have to be based upon habitat types, prey densities, or other criteria. Survey areas can also serve as trend count areas to monitor long-term population status.

This study demonstrated that the track intercept probability estimator can provide useful, relatively

accurate, and precise wolf population estimates. Further refinement of the technique is needed to improve precision, but useful estimates are now attainable if proper conditions exist and experienced personnel are used.

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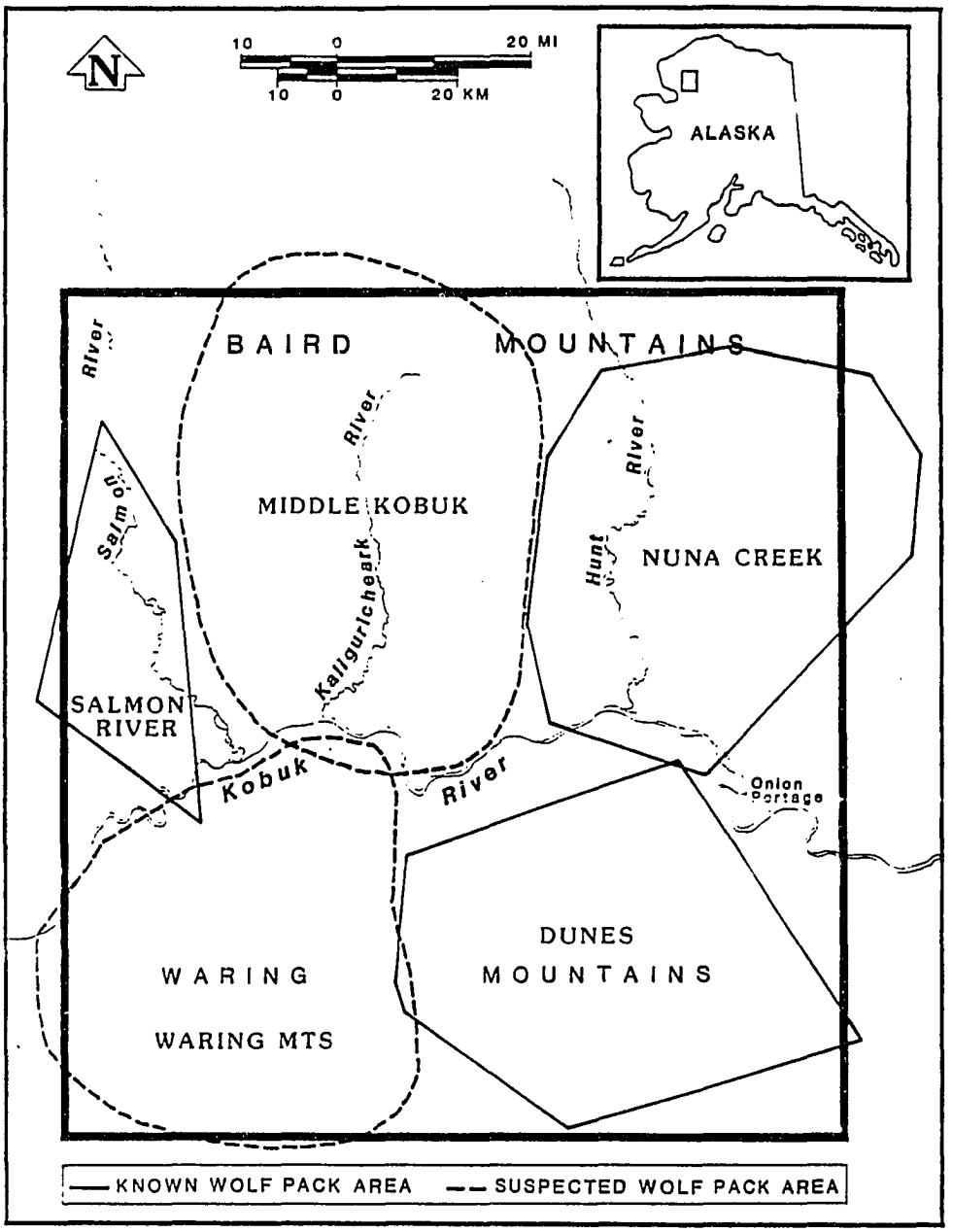


Fig. 1. Boundaries of wolf survey area in relation to observed and suspected territory boundaries of packs in northwest Alaska.

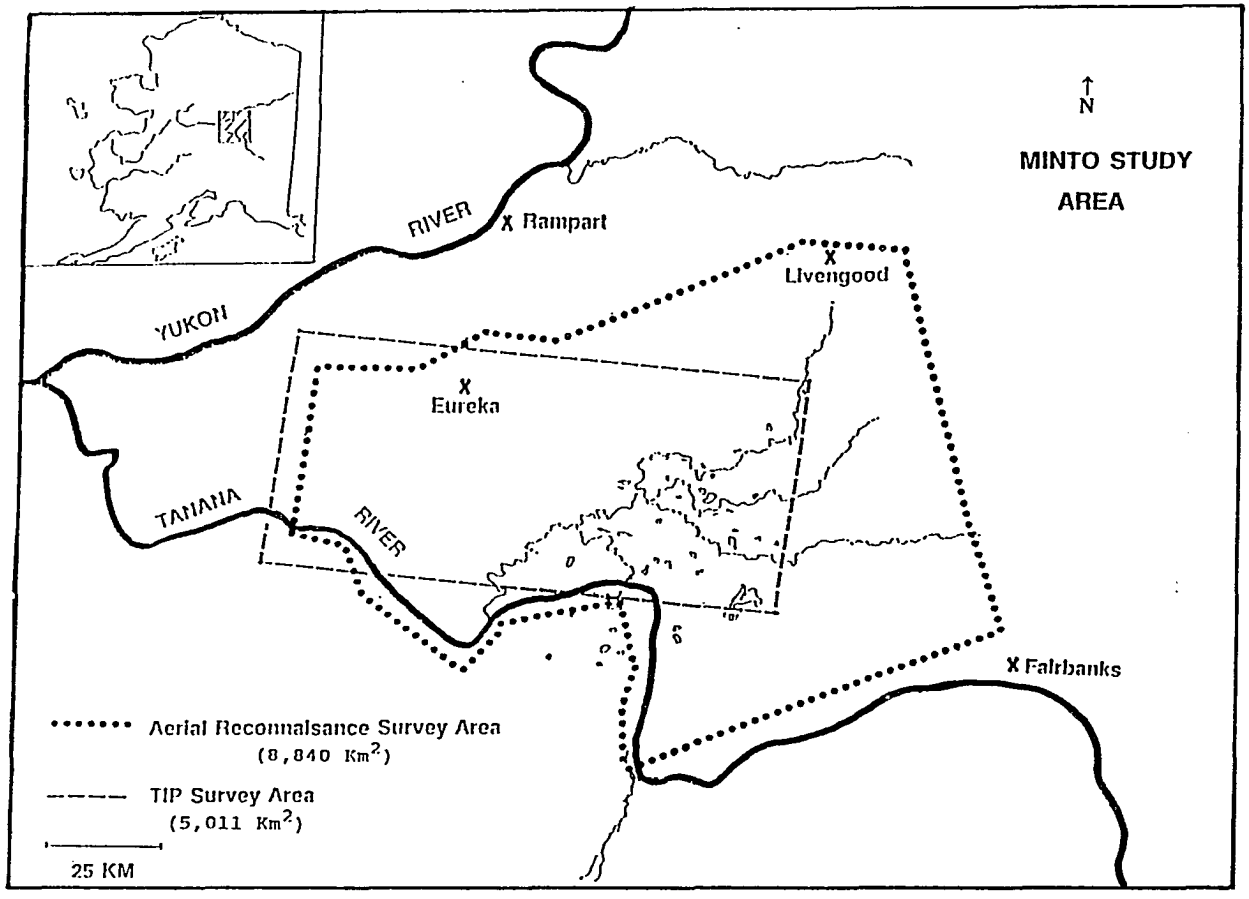


Fig. 2. Relative position of aerial reconnaissance and TIP survey areas in the Minto Study Area in interior Alaska.

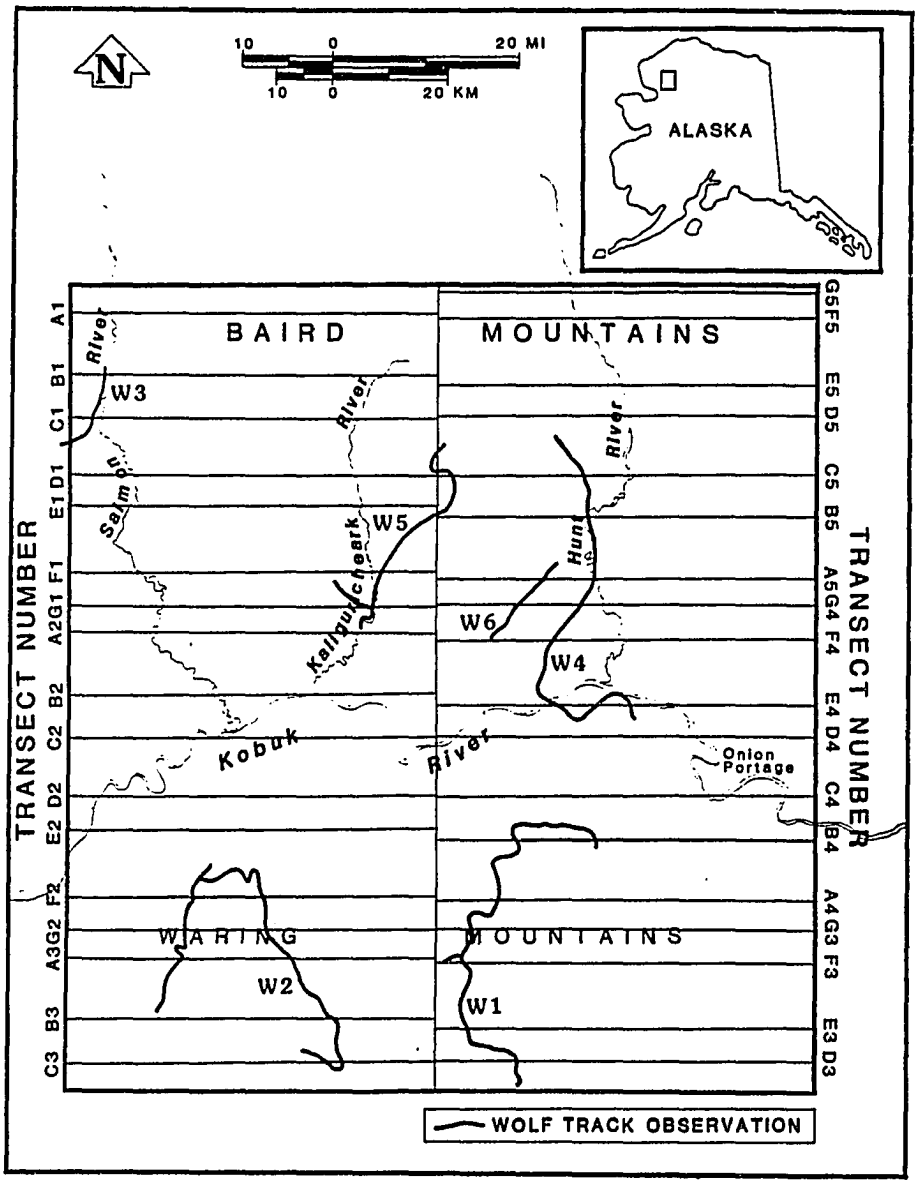


Fig. 3. Location of Transects in northwest Alaska used to survey wolves on 1 May 1990 and observed wolf travel routes.

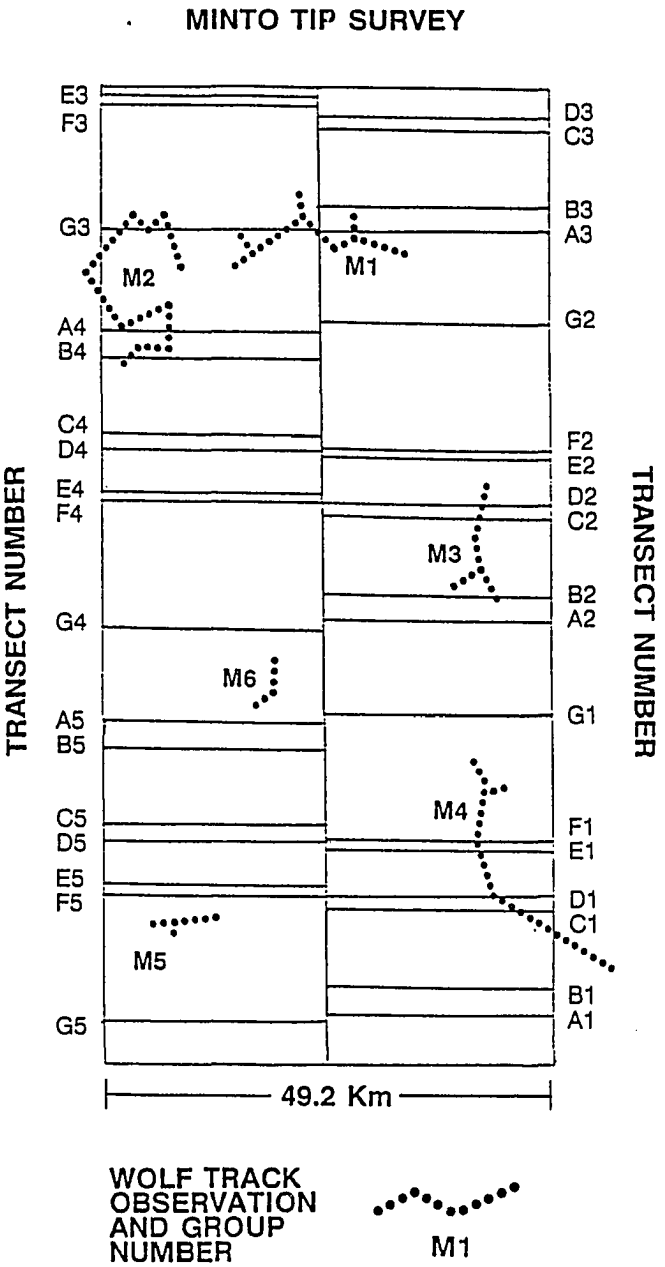


Fig. 4. Distribution of observed wolf tracks in relation to randomly spaced transects in the Minto study area in interior Alaska.

Table 1. Wolf survey data obtained on 1 May 1990 and calculations used to estimate population size within a 6464 km² study area, northwestern Alaska.

Wolf group	Pack Name	Est. no. wolves (no. obs.)	Known no. wolves	Dist. moved (km)	P[1]	T[2]
W1	Dunes	6(2)	5	27.3	0.8258	7.27
W2	Waring	3(2)	3	21.8	0.6591	4.55
W3	Salmon	11(11)	11[3]	8.0	0.2424	45.38
W4	Nuna	16(16)	18	29.3	0.8864	18.05
W5	Kobuk	11(11)	11[3]	19.1	0.5758	19.10
W6	single	1(1)		7.8	0.2348	4.26

Samp. ID	Wolf groups encountered	Pop. est. based on ith sample = sum T for each group
A	W1, W2, W4, W6	34.13
B	W1, W2, W3, W4, W5	94.35

[1] Probability observed (P) = distance moved perpendicular to transect/x-axis X no. of transects.

[2] T = pack size/P.

[3] Ten wolves were observed in each pack prior to survey.

C	W2, W3, W4, W5	87.08
D	W1	7.27
E	W1, W4	25.32
F	W1, W2, W4, W5, W6	53.23
G	W1, W2, W4, W5, W6	53.23
Total		354.61

TOTAL POPULATION ESTIMATE = 354.61/7 = 50.66

80% CONFIDENCE INTERVAL = 33.38 TO 67.94

Table 2. Estimated size and color composition of wolf packs identified within the 8,840 km² Minto Study Area on aerial reconnaissance surveys, 12 March - 2 April 1991.

Pack ID#	Pack name	Estimated number of wolves (no. observed)	Color composition
M1	C.O.D.	2(0)	Tracks only
M2	Montana Creek	6(6)	1 black, 5 gray
M3	Swanneck	12(12)	1 1 black, 1 gray
M4	Dugan Creek	5(3)	1 black, 2 gray
M5	Allen Creek	7(7)	5 black, 2 gray
M6	Hutlinana Creek	6(6)	4 black, 2 gray
M7	Wolverine Mountain	2(0)	Tracks only
M8	Pump 7	3(0)	Tracks only
M9	Tatalina	8(0)	Tracks only
M10	Minto Lakes	4(0)	Tracks only
M11	Uncle Sam	2(1)	1 black
M12	Deadman	2(1)	1 black
M13	Chatanika	3(3)	3 black
M14	Bridge Lake	2(2)	1 black, 1 gray
M15	Bean Ridge	3(0)	Tracks only
M16	Standard	4(0)	Tracks only

Best estimate[a] 64 (41) = 7.2 wolves/1,000 km²

Low estimate[b]58 (39) = 6.6 wolves/1,000 km^2
High estimate[c]71 (41) = 8.0 wolves/1,000 km^2

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[a] Best estimate included packs M1-M14.
[b] Low estimate excluded packs M7, M11, M12, M15, and M16.
[c] High estimate included all packs M1-M16.

Table 3. Summary of wolf survey conducted on 31 March 1991 and calculations used to estimate population size within the 5,011 km^2 Minto Study Area, interior Alaska.

Wolf group	Pack name	Estimated number of wolves (no. observed)	Distance moved (km)	$\underline{P}^a T^b$
M1	C.O.D.	2(0)	6.45	0.16212.34
M2	Montana	6(6)	12.98	0.32618.41
M3	Swanneck	12(12)	12.50	0.31438.22
M4	Dugan	5(2)	20.32	0.5119.79

Sampling ID	Wolf groups encountered	Population estimate based on i^{th} Sample = sum T for each group
A	M1, M2	30.75
B	M2, M3	56.63
C	M3, M4	48.01
D	M3, M4	48.01
E	M4	9.79
F	M4	9.79
G	M1, M2	30.75
TOTAL		233.73

Total population estimate = 233.73 / 7 = 33.39
80% confidence interval = 23.23 - 43.55

[a] Probability observed ($\underline{P}$) = distance moved perpendicular to transect / x-axis X number of transects.

[b] T = pack size / $\underline{P}$.

CHAPTER 3

ACCURACY, PRECISION, AND PERFORMANCE OF SATELLITE TELEMETRY FOR MONITORING WOLF MOVEMENTS

Abstract: We placed 23 satellite platform transmitter terminals (wt = 1.08-1.22 kg) on wolves (Canis lupus) in northwest Alaska during 1987 through 1991. Male and female wolves aged 10-months to 8 years were monitored with no apparent adverse effects on them. We obtained 7374 relocations from the 23 transmitters. Transmitters were programmed to operate 4-6 hours every 2 days and had a mean life span (including days before and after use on a wolf) of 253 days (range = 67-482 days). Average life span while attached to wolves was 181 days (range = 50-366 days). We obtained an average of 29 relocations/month from each transmitter. Accuracy of 1855 relocations at 9 known sites varied among transmitters and averaged 336 and 728 m for best and low quality relocations, respectively. Sixty-eight percentiles for location quality indices (NQ) of 1, 2, and 3 were 734, 556, and 360 m, respectively. The locations from several transmitters exhibited east-west bias in accuracy. Satellite telemetry has great potential for providing improved data sets for evaluation of wolf territory sizes and movements, but lacks accuracy and precision for detailed habitat use assessments. Investigators must carefully

evaluate their objectives to insure use of such technology is appropriate. Costs per satellite relocation averaged about $44 U.S. in comparison to about $166/relocation with conventional telemetry methods using fixed-wing aircraft.

Satellite telemetry has become a widely accepted tool for studying movements of large mammals and birds (Fancy et al. 1988, 1989; Harris et al. 1990), particularly where logistics or movement patterns make conventional telemetry methods costly or unfeasible. In Alaska, the U. S. Fish and Wildlife Service and the Alaska Department of Fish and Game have cooperated since 1984 in a long-term project to develop, test, and refine the use of satellite telemetry for studying large ungulates and predators. Recent advances in transmitter miniaturization and power supplies made use of satellite transmitters feasible in studies of smaller species such as wolves (Canis lupus). In early 1987, Telonics, Inc. (Mesa, Arizona) developed the first satellite transmitter (Service Argos refers to these transmitters as platform transmitter terminals (PTTs) to use 3 "C" size batteries. The 1200 g transmitter package and collar were the smallest available and appeared light enough to be used safely on wolves.

During spring 1987, we used 2 prototype PTTs on gray wolves in northern Alaska (Ballard and Fancy 1988). One PTT failed after 1 month and was removed from the wolf, but the

other performed flawlessly for 13 months (Ballard and Fancy 1988). During 1988-1990, an additional 22 PTTs were used on wolves of various sizes in northwest Alaska. While the study was in progress we determined the accuracy and precision of the position fixes provided by Service Argos for these new PTTs. Several investigators have examined the accuracy and precision of PTTs (Mate et al. 1986, Craighead and Craighead 1987, Fancy et al. 1988, Stewart et al. 1989, Harris et al. 1990, Keating et al. 1991), but only Stewart et al. (1989), Harris et al. (1990) and Keating et al. (1991) evaluated the systems after 1987 when Service Argos made improvements in calculating locations and quality indices (Keating et al. 1991). Of the latter 3 studies, only Keating et al. (1991) evaluated the system while using PTTs as small as ours. We report on the accuracy and precision of the Argos system, and evaluate the performance of PTTs used on free-ranging gray wolves in northwest Alaska during 1987 through 1991.

STUDY AREA

We placed PTTs on free-ranging wolves in northwest Alaska (65° 15', 67° 30' N; 156° 30', 160° 00' W). The area encompassed Kobuk Valley National Park, Selawik National Wildlife Refuge, portions of Noatak National Preserve, and Koyukuk National Wildlife Refuge. The study area has been described by Ballard et al. (1990).

Topography ranges from flat plains along the major river systems (Kobuk and Selawik rivers) to rolling hills in the Waring Mountains and steep mountainous terrain in the Purcell and Baird Mountains. Elevation ranges from near sea level along the rivers to 1231 m in the mountains. Vegetation is varied from unvegetated sand dunes (e.g., Greater and Little Kobuk Sand Dunes), gravel bars, rock screes, and lakes to wetlands and marshes or dense white spruce (Picea glauca) forests along the major river systems. Willows (Salix spp.) occur throughout, but are most common along riparian areas and least common in open tundra. Sparse to dense stands of taiga scrub forest composed of white and black spruce (P. merino) or alpine and arctic tundra are found away from major river systems.

The area has a maritime climate during snow-free periods and long cold periods during winter months. Temperature extremes range from -23° C in winter to 32° C in

summer. Annual precipitation ranged from 380-500 mm in lowland areas to 760 mm in mountainous areas.

METHODS

Fancy et al. (1988) and Harris et al. (1990) provided detailed accounts of the history, use, and applications of the Argos Data Collection and Location System (DCLS). The Argos DCLS is a cooperative effort between the French government, the U. S. National Oceanic and Atmospheric Administration, and the U. S. National Aeronautics and Space Administration. Argos instruments on 2 polar-orbiting satellites pass over Alaska approximately 24 times each day. The satellites receive signals from the PTTs in the ultra-high frequency (UHF) range and relay data to ground stations located in Alaska, Virginia, and France. Data are provided to users monthly on computer tapes. Data can also be accessed approximately 3-8 hours following a satellite overpass using a telephone modem and computer links to the Argos computer (Fancy et al. 1988). For this analysis the term PTT describes the complete package (the satellite transmitter, its' power supply, a VHF tracking beacon and its' power supply, packaging, and the attachment collar) that was placed on the animal.

Each satellite relocation is given a location quality index (NQ) by Argos reflecting its expected accuracy (Table 1). The quality of each relocation depends on the number and quality of messages received during an overpass, the stability of the PTT's oscillator, the geometry of the

overpass, and other factors (Fancy et al. 1988, Harris et al. 1990, Keating et al. 1991). Standard processing by Argos includes only high quality relocations (i.e., NQ's 1-3). Other processing options include non-guaranteed (NQ 0). Non-guaranteed processing provides additional relocations, but the error associated with some of the relocations is not specified by Argos and must be determined by the user. The required processing costs an additional $1.25/day/PTT but provides the greatest number of relocations. However, many relocations are inaccurate with no objective methods for separating accurate from inaccurate relocations. Keating et al. (1991) reported errors ranging from 128 to 396,170 m for NQ 0 relocations. We performed a preliminary analysis of our NQ 0 relocations and also found errors up to several km. Consequently, we excluded these relocations from our analyses and focused only on NQ's 1-3.

A PTT can be programmed to transmit to the satellite with a variety of on/off time periods. The general duty cycle, or programmed pattern of active-inactive transmission periods for our PTTs was 6 hours of transmission every 2 days. Units deployed in 1988 and 1989 transmitted for 6 hours daily through the first 30 days and then 6 hours every 2 days until batteries expired.

We exposed 1-1.5 cm of the UHF antenna on each unit prior to activating each PTT because previous experience

with other PTTs suggested a partially exposed antenna increased location accuracy (S. G. Fancy, U.S. Fish and Wildl. Serv. and W. B. Ballard, Alas. Dep. Fish and Game, unpubl. data). The latter relationship is most directly related to signal strength (W. P. Burger, Telonics, Inc., Mesa, Ariz., pers. commun.). Each collar was cut and the antenna was pulled out so it remained flush up against the collar. Units deployed in 1987 and 1990 had an expected life expectancy of 181 days while those deployed in 1988 and 1989 had an expected life span of 157 days. Two of the PTTs deployed in 1988 (PTT nos. 7913 and 7914) had a 4-hour transmission schedule after the initial 30-day period and their life expectancy was 185 days. There was no significant difference ($\underline{t} = -2.4$, $\underline{P} < 0.05$) in the number of locations provided by 4 or 6 hour transmissions so the data were pooled.

Each PTT contained a mercury tip switch to monitor short and long-term activity, a temperature sensor that provided the internal temperature of each canister, a low voltage indicator to indicate when batteries were becoming depleted, and a conventional very high frequency (VHF) transmitter to allow each animal to be relocated by conventional radio telemetry. The UHF and VHF transmitters had separate power supplies and antennas. Descriptions of temperature and activity sensors and wolf activity patterns

as determined by satellite telemetry are described by Fancy and Ballard (this volume).

Four generations of PTT collar design were used during the study. The initial prototype PTT used in 1987-1988 weighed 1.22 kg, was rather bulky, and could only be deployed on adult wolves. Modifications have involved reducing the size and weight of the units. The first modification involved eliminating the urethane shock buffer from the front and rear of the canister housing the transmitter. The sides of this second generation PTT (1.16 kg) were encased in urethane to protect the antenna as they exited the canister before entering the collar. On several collars the urethane had separated from the canister. If glass to metal feed troughs for the antennas were broken as the urethane separated from the canister water could potentially enter the unit. For the third generation (1.08 kg), the urethane caps were eliminated and the antennas exited the top of the canister directly into the collar. The fourth generation (1.10 kg) involved narrowing the depth of the canister and the collar.

Wolves were immobilized for deployment of PTTs by darting from helicopters using methods described by Ballard et al. (1982, 1991b). Conventional VHF transmitters were deployed on 1 to 3 other members of a pack to aid in locating the pack and the individual with the PTT.

Prior to deployment, when wolves died, and after the PTTs had been retrieved, they were allowed to continue transmitting from fixed known locations (Table 2). With the exception of the Nome PTTs that transmitted indoors, all other PTTs were unobstructed, transmitted from the ground, and were not on a wolf. Service Argos requires that an average elevation of transmission be designated prior to deployment. The designated elevation for this study was sea level. Known locations were determined from 1:63 360 scale U. S. Geologic Survey maps. Satellite and known locations were converted to Universal Transverse Mercator (UTM) coordinates and differences between them were calculated using LOTUS worksheets.

Statistical Tests

We analyzed locations with NQ's 1-3 separately because all previous studies have found significant differences in location errors among each NQ category. For each NQ category, we used each combination of PTT, year, and known location as a treatment. Homogeneity of variances was tested within each NQ category with Bartlett-Box F test (Snedecor and Cochran 1973). Unequal variances were found ($P < 0.001$) within each category. Differences among treatments by NQ category were then analyzed using the Kruskal-Wallis test (Ott 1988). If significant differences

($P < 0.05$) were detected, we performed multiple comparison of treatment means using Mann-Whitney U tests (Ott 1988).

Location errors were compared among locations for each PTT within the same year using Mann-Whitney tests (Ott 1988). Results of these analyses were pooled, and we report differences using Fisher's combined probability tests of significance (Sokal and Rohlf 1969). Location error was also evaluated by year using the same statistical procedures described above by comparing errors for each PTT positioned at the same site between years. Proportional distributions were analyzed using log-linear models and Chi-square analyses of log-transformed odds ratios. Directional error and bias were measured with Hotelling's one-sample test (Batschelet 1981:144). Because of differences in location errors among transmitters and locations, differences in location quality, and whether the PTTs were transmitting on or off of a wolf, different subsets of data were tested for each analysis. Consequently, comparisons among tables will reveal discrepancies among some data sets.

RESULTS

Performance

During 1987-1990, we deployed 23 PTTs on wolves of both sexes ranging in age from 10 months to 8 years and in weight from 28.6 to 51.7 kg (Table 3). Subsequent visual observations from fixed-wing aircraft and physical examinations during re-collaring suggested none of the wolves was adversely affected by the size or weight of the PTTs. Collars (50.0-68.3 mm in width) caused excessive rubbing of guard hairs and underfur and would probably significantly reduce the value of the hides of animals shot or trapped and commercially sold.

Average total life span (includes periods on and off wolves) for the 23 wolf PTTs used during 1987 through 1991 was 253.1 ±127.5 (SD) days (range = 67-482 days)(Table 3). Average life span while actually on a wolf, including wolves that died prior to PTT failure was 181.2 ±111.7 days (range = 50-366 days, n = 23). The latter value did not differ from an average life span of 186.7 ±108.7 days (range = 50-366 days, n = 14) for PTTs that expired while attached to a wolf. The latter 2 values were similar to the theoretical life span predicted by Telonics based upon battery life with a duty cycle of 6 hours on and 42 hours off. Longer life spans for PTTs not attached to animals have been reported previously by Fancy et al. (1988) and Harris et al. (1990).

Variance in life spans of PTTs depend primarily on variability among individual battery packs, specific current drains of electronics, repetition periods, duty cycles, operating temperatures, and standing voltage wave ratios. The latter term refers to the proximity of the antenna to the animal. Close proximity causes the antenna to become detuned. Power output of the PTT automatically adjusts to overcome antenna detuning, and consequently, can increase battery drain by up to approximately 20% (S. M. Tomkiewicz, Telonics, Inc., Mesa, Ariz., pers. commun.).

Average life spans for PTTs that ceased operation while attached to wolves differed significantly by year of deployment ($H = 5.4$, $P = 0.067$). Excluding the 1987 prototype PTT ($n = 1$, 319 day actual life span), average life span for this subset of PTTs declined each year of study (Table 3): 1988 = 259.3 $\pm$86.3 days ($n = 4$), 1989 = 211 $\pm$106.1 days ($n = 5$), and 1990 = 104.2 $\pm$ 65.2 days ($n = 5$). Units deployed in 1988 had significantly longer ($Z = -2.20$, $P = 0.027$) life spans than those in 1990, but not those in 1989 ($Z = -0.73$, $P = 0.462$). Although life spans in 1989 and 1990 were not significantly different ($Z = -1.57$, $P = 0.117$), the 1990 values were lower. Both 1988 and 1989 PTTs exceeded the theoretical life span of 157 days, but the life spans of 1990 PTTs were considerably shorter (i.e., 104 versus 181 days). Although the canister design was

different between 1989 and 1990 design differences should not have effected operation of the PTTs. Premature battery failure or failure of sockets which connect microprocessors to the main board could have been responsible for the declining life span (W. P. Burger, pers. commun.).

During 1990 wolf number 55 died of rabies in early June. After the wolf died and remained motionless for several days, the PTT ceased transmitting to the satellite. When the PTT was retrieved, successful transmission was resumed. Telonics examined the PTT and was unable to duplicate the failure, and could not detect any problems. It was possible that the antenna radiation pattern on the dead wolf prevented signal reception at the satellite (W. P. Burger, pers. commun). Also, faulty microprocessor plugs and possibly variation in batteries were suspected as the possible reasons for premature failure of PTTs deployed on grizzly bears (Ursus arctos) in northwest Alaska during the same time periods as this study (Ballard et al. 1991a, W. P. Burger and D. Decker, Telonics, Inc., Mesa, Ariz., pers. commun.). Other researchers (J. L. Weaver, Univ. Montana and P. C. Paquet, Jasper Natl. Park, Alta., pers. commun.) also had shorter life spans for PTTs manufactured in 1990 (n = 2) versus those manufactured in 1989 (n = 2).

Very high frequency transmitters in the PTT canister were inferior to conventional VHF transmitters in terms of

distance that radio signals could be received by fixed-wing aircraft. J. Weaver (pers. commun.) reached a similar conclusion for similar PTTs. Initially, most VHF signals from PTTs could be received from an aircraft at a distance of 10-20 km, but reception distance declined with time. When the UHF units expired, the VHF transmission distance was <1 km, and in several cases the units could not be heard until the aircraft flew directly over the transmitter. Unless the PTT-equipped wolf was accompanied by other wolves equipped with conventional VHF transmitters, relocation of animals by the PTT VHF transmitter was nearly impossible.

The VHF and UHF units are contained within the same canister on the same collar rather than in two separate canisters. Because of neck size the length of the VHF antenna is compromised (i.e., reduced from 457 mm to 229 mm) resulting in a reduction in transmission range of approximately 75%. Keating et al. (1991) suggested that signals from each unit might interfere with each other and result in both poorer quality satellite relocations and reduced range from the VHF unit. However, there appears to be no basis for this hypothesis, and the relatively short antenna explains the lack of range of the VHF transmitter (S. M. Tomkiewicz, pers. commun). Unless the range on the VHF transmitter can be significantly improved future investigators might consider removing them from the unit to

lighten the PTT. Elimination of the VHF unit would lighten the PTT by approximately 75 g. If "C" cell batteries could be replaced by "D" cell batteries the life span of the PTT could theoretically be increased. However, the increase in weight would be approximately 100 g (W. P. Burger, pers. commun.).

During April 1987 through May 1991, signals from the 23 PTTs on wolves were received by satellite during 14,669 overpasses and 7374 relocations (NQ's 0 - 3) were calculated. An additional 7295 sets of sensor data without relocations were obtained. Satellites received an average of 1.49 signals/overpass in which at least one signal was received. Fewer relocations/month were obtained for each PTT when deployed on a wolf than when free-standing (X^2 = 1473, $P < 0.001$). An average of 28.5 $\pm$18.4 relocations (n = 106 months) with sensor data was provided per month of transmission while attached to the wolf compared to 50.5 $\pm$29.0 relocations/month (n = 31 months) when not attached. We obtained 3801 relocations ranging in quality from NQ 1-3 from the 23 PTTs used on free-ranging wolves; NQ 1 = 2869, NQ 2 = 879, and NQ 3 = 53. Each PTT transmitted (in contrast to life span that includes both transmission and non-transmission days) an average of 71.7 days $\pm$46.4 (range = 9-148 days) and provided an average of 2.2 $\pm$0.7

relocations/day of transmission (range = 1.2-3.9 relocations).

Accuracy and Precision

Average location error for NQ's 1-3 for all PTTs (n = 16) at 9 known locations during 3 years of deployment was 718 ±871.5 m (n = 2597). Mean errors for locations with NQ's 1, 2, and 3 were 848 ±942, 563 ±533, and 329 ±219 m, respectively. However, we found significant differences among PTTs by location, year of deployment, and NQ category.

For NQ 1's, there were significant differences among PTTs for the Nome relocations (H = 15.2, P = 0.0189) but not for the other locations. Selawik Cabin during 1989 did approach significance (H = 12.5, P = 0.084). Similarly for NQ's 2 and 3, there were no significant differences among PTTs by location and year (H ranges = 1.56-12.82, P = 0.171-0.955), except for Nome relocations (H ranges = 14.79 - 16.60, P = 0.005 - 0.011). We compared individual PTTs for the Nome relocations and found 11 of 21 possible comparisons were significantly different (Mann-Whitney U test, P = 0.018 - 0.075). Nome PTTs were the only ones to transmit from inside a heated building, and the large errors may have been caused by a combination of temperature and the shielding of signals from over-flying satellites caused by the 2-story building. Nome relocation errors ($\bar{x}$ = 812.5 ±985.4 m) were

significantly larger ($\underline{t}$ = 31.4, $\underline{P}$ < 0.001) than those from other locations ($\underline{x}$ = 577.1 m) and were excluded from further analysis.

We found significant differences ($\underline{P}$ < 0.05) for location errors among PTTs even after we excluded Nome relocations. However, there were no significant differences in location errors by NQ for location (NQ 1 $\underline{P}$ = 0.53, NQ 2 $\underline{P}$ = 0.84, and NQ 3 $\underline{P}$ = 0.42) or year of deployment (NQ 1 $\underline{P}$ =0.23, NQ 2 $\underline{P}$ = 0.73, and NQ 3 $\underline{P}$ = 0.95) when each PTT was analyzed separately. Average location error for all PTTs excluding Nome relocations was 728 ±757, 551 ±528, and 336 ±220 m for NQ's 1 through 3, respectively (Table 4). Average error by location ranged from an average of 259 m for NQ 3 at Kateel River to 1049 m for NQ 2 at Kotzebue, Alaska (Table 5). Sixty-eight percent of the relocations were <734, <556, and <360 m from the known location for NQ's 1 through 3, respectively.

We compared the frequency of relocations by NQ for PTTs on and off the wolf (Table 6). A three-way log-linear model (PTT X NQ class X on or off animal) was fitted to examine whether the distribution of relocations between NQ codes was independent of the PTT and/or whether the PTT was on or off a wolf (Agresti 1984). The full model could not be rejected ($\underline{P}$ < 0.001) indicating the distribution of NQ codes was not independent of PTT nor whether it was deployed on or off of

a wolf. Location quality code distributions differed among PTTs when the collar was on or off a wolf. As an exploratory measure, a two-way log-linear model (PTT X NQ class) was fitted to NQ code distributions for when PTTs were deployed on wolves, and a separate model for when PTTs were not on wolves. Neither full two-way model was rejected ($P < 0.001$ and $P < 0.001$, respectively) indicating that the distribution of NQ codes was not independent of PTT in either case.

In order to provide some comparison of expected distributions of NQ codes when PTTs were deployed on wolves versus when they were not, we computed and analyzed odds ratios for NQ = 3 versus NQ < 3 and NQ = 1 versus NQ > 1 (Table 6; Fleiss 1981). For 18 of 20 PTTs, NQ = 1 was significantly more likely ($P < 0.05$) when a collar was used on a wolf than when it was not. For 19 PTTs, NQ = 3 was significantly less likely ($P < 0.05$) when a collar was used on a wolf than when it was not. In general, the odds that a relocation was NQ = 3 was 13 times less likely when the PTT was used on a wolf and NQ = 1 was about 5 times more likely, however, the odds ratios for NQ =1 failed the test of homogeneity.

There were significant directional error biases in locations reported for different PTTs and locations ($P < 0.05$) (Table 7 and Figs. 1-3). Generally, locations

provided by the Argos system were biased towards the south and west. All NQ 2 and 3 relocations with the exception of those from Shungnak had significant directional biases ($P < 0.05$), 71 percent of which were towards southerly and westerly directions. Surprisingly, NQ 1 relocations for both Selawik and Kotzebue were not significantly ($P > 0.05$) biased.

Lastly, we tested the hypothesis that the accuracy of relocations could be improved by slightly exposing the UHF antenna outside of the collar material. We placed 1 PTT on a domestic dog at a known location (termed experiment 1), and after several days of transmission, we exposed the UHF antenna and the PTT was again allowed to transmit (experiment 2). We then removed the PTT from the dog and allowed the PTT to transmit from the same location (experiment 3). Significant differences in location error were found between experiment 1 ($\bar{x}$ = 3695 $\pm$1829 m, n = 30) and experiments 2 ($\bar{x}$ = 2624 $\pm$774 m, n = 23) and 3 ($\bar{x}$ = 2268 $\pm$450 m, n = 20)(Mann-Whitney U test, $P < 0.002$). No differences were detected between experiments 2 and 3 ($P = 0.64$). These analyses suggest exposing the UHF antenna can improve the quality of relocations.

DISCUSSION

Numerous factors influence the accuracy of relocations obtained with satellite telemetry. Harris et al. (1990) reported that PTT oscillator instability, changes in PTT elevation, animal movement, insufficient number of transmissions reaching the satellite, errors in satellite orbital data, computational algorithms, or mapping methods affected location accuracy. Fancy et al. (1988) and Harris et al. (1990) also found that changes in ambient air temperature, antenna size, deployment on animals versus transmission from inanimate positions, and maximum satellite elevation during an overpass affected accuracy of satellite relocations. Harris et al. (1990) reported that there may be an interaction among PTT, satellite overpass, and whether the PTT was on or off an animal with regard to reductions in precision of relocations. Keating et al (1991) reported similar results. Our findings agree with those of Fancy et al. (1988), Harris et al. (1990), and Keating et al. (1991) concerning factors that influence accuracy and precision.

Directional bias in satellite locations has been reported in all studies that have evaluated accuracy and precision of satellite telemetry (Fancy et al. 1988, Harris et al. 1990, and Keating et al. 1991). Fancy et al. (1988) reported west and northwest biases while Keating et al. (1991) reported longitudinal biases primarily in a

southeasterly direction. Fancy et al. (1988) suggested that part of the bias could be the result of using U. S. Geological Survey topographic maps, which use the NAD27 projection of the earth whereas Argos uses the WGS84 system. However, Harris et al. (1990) reported that even after adjusting the data to account for the differences in the two projections, significant biases continued to occur, but errors were relatively small (i.e., <150 m) in relation to total variation. Keating et al. (1991) also adjusted for type of map projection and concluded that directional errors were largely caused by distance from satellite and differences in estimated and actual PTT elevation. P. Y. Letraon (Service Argos, Landover, Md., unpubl. data) estimated that errors in calculated locations could be 0.5-3.5 the error in actual versus assumed altitude of the PTT. Because our baseline altitude was at sea level and most of the PTTs were tested at Selawik cabin (Table 2) this source of error should have been minimal in this study.

Keating et al. (1991) reported 68 percentile errors of 1188 m, 903 m, and 361 m for NQs 1 through 3, respectively in comparison to expected precision (Service Argos 1984, Clark 1989) of 1510 m, 528 m, and 226 m, respectively. Our errors of 556 m and 360 m for NQ's 2 and 3, were similar to those reported by Service Argos (1984) and Keating et al. (1991), but our mean error of 734 m for NQ 1 was

considerably lower than those reported previously. Some of the reported differences were due to a less rigorous study design than that of Clark (1989) or Keating et al. (1991) and because Argos estimates were based upon independent distributions of x and y coordinates whereas our estimates were based on joint distributions. Also, relatively small sample sizes may have influenced our results. For example, 36% of the relocations reported in Table 5 for NQ 1 were from one PTT. Additionally, our collars were configured differently than those used in previous studies, and our study was conducted farther north than the other studies. Therefore, system performance should have benefitted from a higher number of total overpasses and overpasses with good pass geometry than at lower latitudes. We should have had more locations with more overpasses and a higher probability for getting more NQ 3 locations.

Potentially large variation in location errors among wolf PTTs could create problems in data interpretation depending upon study objectives. Users of wolf PTTs cannot afford the time or funds to conduct accuracy and precision checks for each study area and individual PTT. At the very least, however, users of wolf PTTs should allow each PTT to transmit for several days prior to deployment so gross differences in PTT accuracy can be assessed.

Keating et al. (1991) stated that use of satellite

telemetry for assessing "localized movements and habitat use" is an alluring alternative to using conventional telemetry methods, but substantial improvements in the quality of the data are necessary before such studies can be conducted. We add, it is also a method that has become "in vogue" and prestigious to use even though some study objectives might be more efficiently accomplished with conventional telemetry or other methods. Even assuming average location errors of 300-700 m, such data have limited use unless an investigator is only interested in broad habitat associations. However, assessing localized movements and habitat use is a matter of scale that is dependent upon the species being studied and its' landscape. If patches of prey or habitat are distributed coarsely (i.e., >2 km) across a landscape and the study animal moves great distances each day (e.g., 10-20 km/day) then satellite telemetry may provide data of sufficient precision to allow assessment of habitat use.

Investigators must carefully consider study objectives before deciding to use satellite telemetry. In our case, use of satellite telemetry appeared justified because weather, short daylight, and logistics during winter precluded us from locating wolves frequently enough with conventional telemetry methods to accurately determine their movement patterns. In northern latitudes, wolves either

occupy large territories (i.e., 1000 to 2000 km^2) or they travel long distances following migratory caribou (Rangifer tarandus). In our study area there was a high probability that some wolves could potentially move hundreds and possibly thousands of kilometers while following migratory caribou. Maintaining radio contact with them would be difficult and perhaps impossible. Location errors of the magnitude reported in our wolf study are probably acceptable for estimating wolf territory sizes or tracking animal movements. Territory sizes and movement characteristics are probably more accurately enumerated with satellite telemetry than with conventional radio-telemetry methods because of the continuous uniform monitoring. A preliminary analysis for 1 wolf pack indicated the annual territory size determined by satellite data (n = 415) was approximately 75% larger than that found through conventional radio-telemetry methods (n = 38) (Ballard and Fancy 1988). Relocations obtained with conventional telemetry methods are often clumped, auto-correlated, and too infrequent to accurately assess territory or home range sizes.

We compared costs associated with using satellite telemetry versus conventional radio-telemetry using fixed-wing aircraft. PTTs in 1992 cost $3500 (U.S.)/unit and can be refurbished for approximately $800/unit. Data processing costs from Service Argos are based upon the equivalent of a

PTT transmitting 1-6 times each day for 1 year (PTT-year). Each PTT-year costs $4000 and the fee for special animal process costs an additional $1.50/day/PTT. Each conventional VHF radio collar costs $330/unit and has a life span of approximately 3 years. We assumed each wolf pack would contain a minimum of 3 collars; 1 PTT and 2 VHF collars for the PTT equipped pack and 3 conventional collars for the VHF equipped pack. Each PTT equipped pack would be visually observed 6 times/year to collect data on productivity, den site locations, and mortality, only standard normal processing would be used (requires 0.5 PTT-year of data processing), and each PTT would transmit 6 hours every 2 days for 6 months or longer (requires one recapture per year). We also assumed a study duration of 3 years, capture costs of $1000/individual, and 1 hour of fixed-wing aircraft charter ($140/hour) per relocation for VHF equipped packs (W. B. Ballard, Alas. Dep. Fish and Game, unpubl. data). Using the above assumptions the average annual cost to maintain a PTT and 2 VHF transmitters in a wolf pack over a 3-year period was $7327. Assuming the PTT transmitted an average of 6 months and provided an average of 28 relocations/month (168 locations), the average cost/relocation was $44. To attain the same number of relocations with conventional VHF telemetry each relocation would cost about $148. Assuming a more realistic monitoring

intensity of once/week, the average annual cost/relocation was $166.

Cost per relocation was cheaper for both methods when a greater number of relocations were obtained per year. For an average wolf study lasting 3 years and requiring 50 relocations per year, costs per relocation were $147 and $172 for PTT and VHF transmitter equipped packs, respectively. Differences between the 2 methods increased as the total numbers of relocations/year increased. At 200 relocations/year average cost/relocation was $37 and $147, respectively while for 400 locations average cost was $22 and $144, respectively. Reasons for these large differences include high initial costs for wolf PTTs but subsequently low monitoring costs in comparison to low initial costs for conventional VHF transmitters, but relatively high fixed monitoring costs (1 hour charter aircraft/relocation). Clearly, use of satellite telemetry is cost effective for obtaining large quantities of movements and relocation data, and may also provide indications of activity patterns once additional effort has been made to calibrate and categorize such data (Fancy and Ballard this volume).

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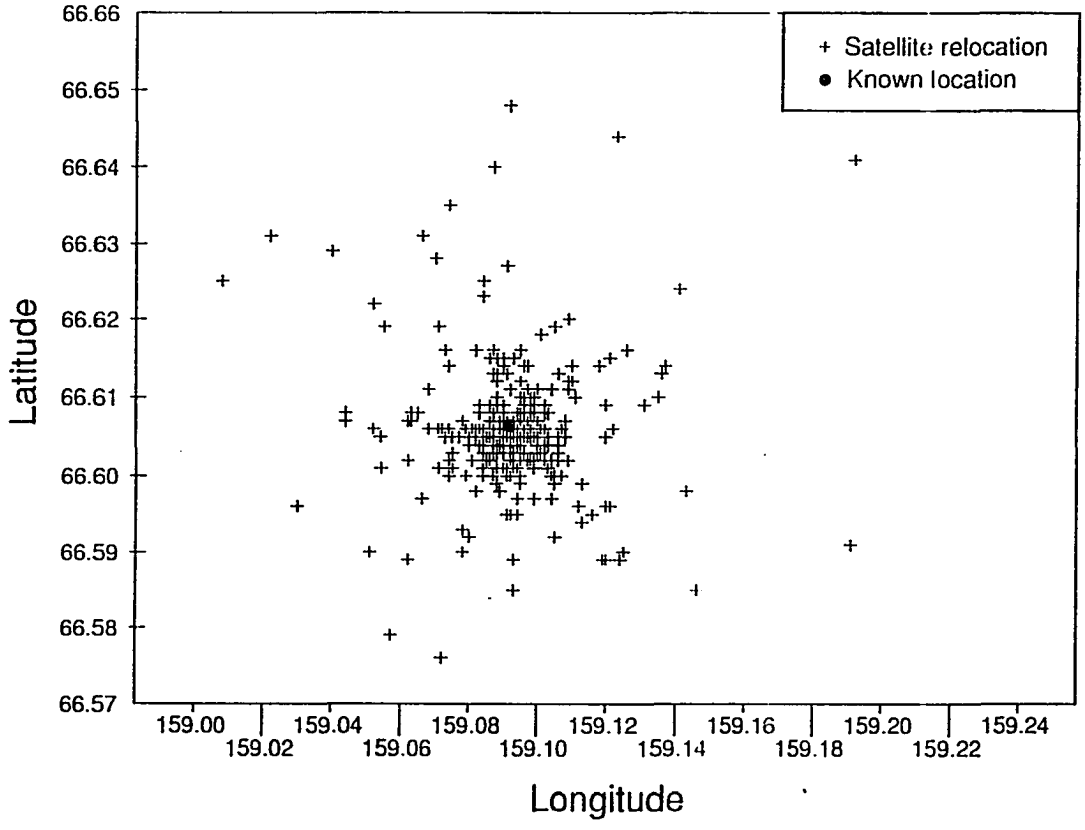


Fig. 1. Scatterplot of location quality index (NQ) 1 relocations provided by several wolf Platform Transmitter Terminals (PTTs) in relation to known location at Selawik Cabin in northwest Alaska during 1988 through 1990. Average directional bias was 195°; not significantly different from zero ($\underline{P} > 0.05$).

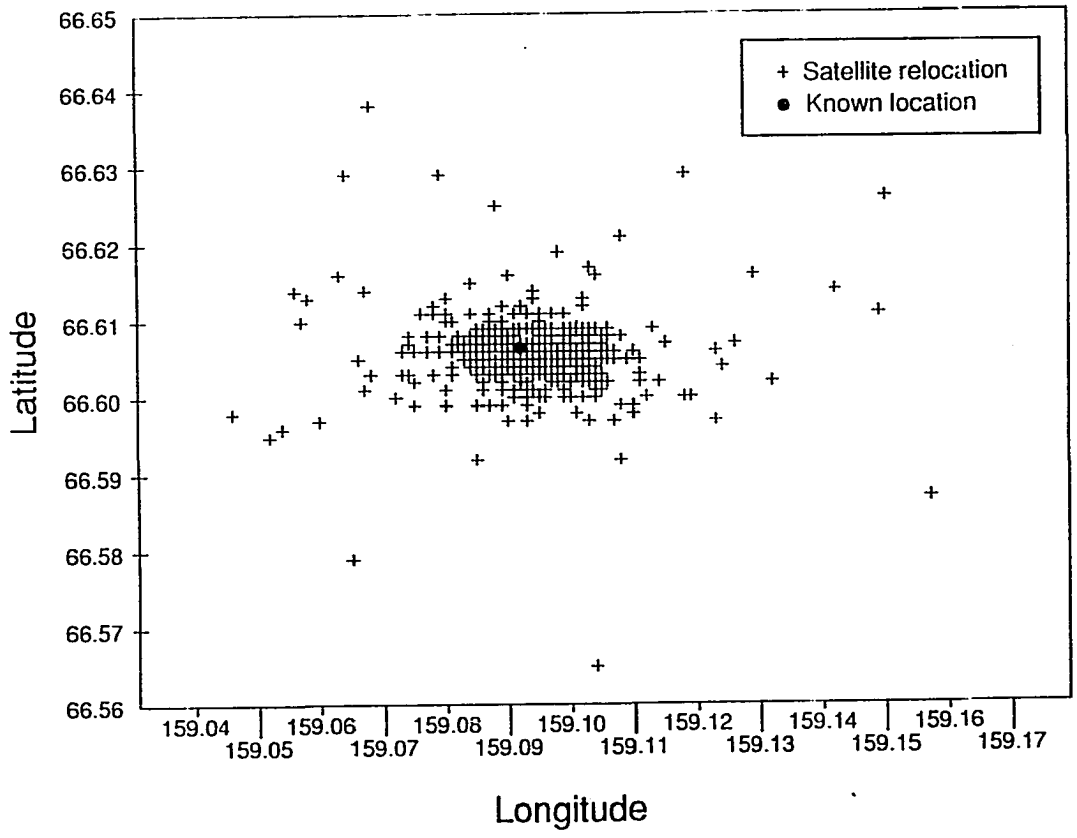


Fig. 2. Scatterplot of NQ 2 relocations provided by several wolf PTTs in relation to known location at Selawik Cabin in northwest Alaska during 1988 through 1990. Average directional bias was 211°; significantly different from zero ($\underline{P} < 0.05$).

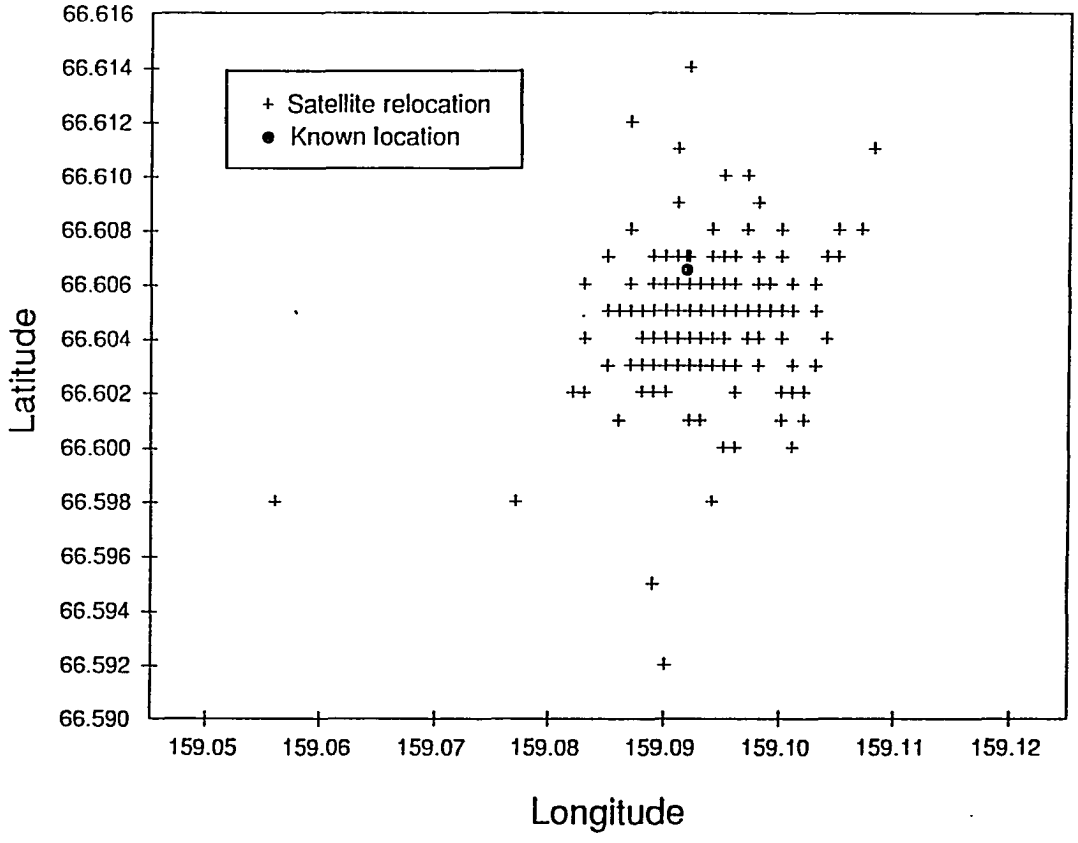


Fig. 3. Scatterplot of NQ 3 relocations provided by several wolf PTTs in relation to known location at Selawik Cabin in northwest Alaska during 1988 through 1990. Average directional bias was 195°; significantly different from zero ($\underline{P} < 0.05$).

Table 1. Description of location quality indices (NQ) used with locations obtained from PTTs by Service Argos (1989).

NQ Index	Description
3	>4 messages received and pass duration >420 seconds. Good internal consistency (<0.15 Hz) and pass geometry (5°<DT<18°). Good quality control on oscillator drift and unambiguous solution. Locations reportedly accurate within 150 m for 68% of occasions.
2	>4 messages and pass duration >420 seconds. Good internal consistency (<1.5 Hz) and geometric conditions (1.5°<DT<24°). Good quality control on oscillator drift and unambiguous solution. Locations reportedly accurate within 350 meters for 68% of occasions.
1	≥4 messages and 240 s <pass duration <420 s or only one test to determine correct solution. Good internal consistency (1.5 Hz) and geometric conditions (1.5°<DT<24°). Location reportedly accurate within 1000 m for 68% of occasions.
0	Messages ≥2, no minimum time required or rejected location. Quality of results to be determined by user. Two possible locations are provided.

Table 2. Known locations in northwest Alaska used to assess accuracy and precision of satellite radio collars.

Location name	Elevation (m)	Latitude - Longitude (decimal degrees)	No. PTTs tested
Nome	0	64.4971N - 165.4008W	8
Kotzebue	0	66.8987N - 162.5970W	2
Selawik Cabin	1	66.6065N - 159.0918W	16
Kiliovilik River	19	66.4641N - 158.6720W	1
Icy View (Nome)	39	64.5012N - 165.3891W	1
Shungnak	45	66.8880N - 157.1359W	1
Kateel River	91	65.3315N - 158.5909W	1
Pick River	34	66.5219N - 156.4340W	1
Rabbit Mountain	36	66.6361N - 158.8071W	1

Table 3. Summary of statistics associated with deployment of wolf satellite PTTs and their transmission life span during 1987 through 1991 in northwest Alaska.

PTT no.	Wolf no.	Pack	Sex	Age	Weight (kg)	Total Life Span		Life Span on Wolf		Status[1]
						Dates	No. days	Dates	No. days	
7900	001	Rabbit Mt	M	2 yr	43.2	17 Apr 87- 27 Apr 88	377	17 Apr 87- 29 Feb 88	319	1
7909	007	Jade Mt	F	Ad	37.6	07 Apr 88- 21 Feb 89	321	25 Apr 88- 21 Feb 89	303	3
7909	067	Pick Rv	F	Yrl	39.0	23 Mar 90- 21 Feb 91	336	14 Apr 90- 28 Jun 90	76	2
7910	016	Ingruksukruk	F	Yrl	28.6	26 Apr 88- 13 Aug 88	110	26 Apr 88- 13 Aug 88	110	3
7910	037	Pick Rv	F	3 yr	44.9	05 Apr 89- 11 Jul 89	98	15 Apr 89- 11 Jul 89	88	3
7911	012	Purcell Mt	F	Ad	33.1	03 Jun 88- 19 Apr 89	321	13 Jun 88- 19 Apr 89	311	3
7912	010	Nuna Ck	F	Ad	47.6	23 Apr 88- 06 Mar 89	318	28 Apr 88- 06 Mar 89	313	3
7912	072	Upper Tag	F	Yrl	39.0	17 Mar 90- 17 Jun 90	93	17 Apr 90- 17 Jun 90	93	3
7913	024	Pick Rv	M	Ad	47.6	08 Nov 88- 09 Jul 89	244	16 Nov 88- 18 Feb 89	95	1
7913	074	Ingruksukruk	M	3 yr	49.4	17 Mar 90- 05 Jun 90	81	17 Apr 90- 05 Jun 90	50	3
7914	014	Rabbit Mt	F	Ad	44.9	24 Apr 88- 16 Feb 89	299	26 Apr 88- 16 Feb 89	297	1
7914	032	Kiliovilik	F	Yrl	36.7	04 Mar 90- 13 Apr 91	406	18 Apr 90- 11 Jun 90	55	2

PTT no.	Wolf no.	Pack	Sex	Age	Weight (kg)	Total Life Span		Life Span on Wolf		Status[1]
						Dates	No. days	Dates	No. days	
10908	030	Rabbit Mt	F	2 yr	37.2	07 Apr 89– 18 May 90	407	10 Apr 89– 03 Jan 90	269	2
10909	048	Kateel Rv	M	8 yr	51.7	08 Apr 89– 21 Mar 90	348	14 Apr 89– 25 Jun 89	73	4
10910	033	Dunes	F	3 yr	47.2	07 Apr 89– 01 Feb 90	301	10 Apr 89– 01 Feb 90	298	3
10911	002	Purcell Mt	F	4 yr	45.4	05 Apr 89– 07 Aug 89	125	14 Apr 89– 07 Aug 89	116	3
10912	040	Ingruksukruk	F	Pup	34.5	08 Apr 89– 19 Oct 89	195	14 Apr 89– 19 Oct 89	188	3
10913	046	Upper Tag	F	Pup	38.1	04 Apr 89– 29 Jul 90	482	14 Apr 89– 14 Apr 90	366	5
10914	033	Dunes	F	4 yr	47.2	17 Mar 90– 13 May 91	423	18 Apr 90– 27 Feb 91	317	1
10915	064	Purcell Mt	F	Ad	39.9	23 Mar 90– 01 Dec 90	254	18 Apr 90– 01 Dec 90	228	3
10916	057	Salmon Rv	F	4–5 yr	50.8	23 Mar 90– 21 Jul 90	121	14 Apr 90– 21 Jul 90	99	3
10917	055	Nuna Ck	F	2 yr	46.7	25 Mar 90– 27 Jun 90	95	14 Apr 90– 05 Jun 90	53	2
10918	050	Kiliovilik	M	Ad	40.4	29 Mar 90– 03 Jun 90	67	14 Apr 90– 03 Jun 90	51	3

[1]Status of wolves at time that radio ceased transmission: (1) wolf killed by hunters and transmitter prematurely removed, (2) died of rabies and transmitter prematurely removed, (3) transmitter life fully realized, (4) dropped collar and transmitter prematurely removed, and (5) transmitter removed during recollaring (transmitter life fully realized).

Table 4. Summary of average location error of 16 wolf PTTs transmitting from known fixed locations in northwest Alaska during 1988 through 1991.

	Quality of Relocation[1]											
	NQ1			NQ2			NQ3			ALL		
Radio No.	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
1	930	1169	65	722	498	56	457	309	28	763	855	149
2	818	621	34	595	581	83	341	198	74	536	508	191
3	1009	1176	17	1100	910	14	280	190	6	925	1001	37
4	1049	992	29	586	410	45	409	220	21	688	667	95
5	815	570	102	656	553	53	422	204	26	712	544	181
6	421	329	114	370	196	37	477	384	15	415	310	166
7	550	836	8	556	609	8	452	151	4	533	632	20
8	704	623	13	592	429	14	452	252	4	621	498	31
9	1283	1140	10				256	40	2	1112	1106	12
10	497	270	7	456	179	9	342	86	4	448	202	20
11	589	586	282	368	267	202	263	139	191	431	435	675
12	811	823	25	619	700	33	407	197	12	657	703	69
13	1188	853	29	557	679	36	384	164	7	794	791	72
14	1026	984	19	808	992	38	384	318	6	834	952	63
15	1405	1560	14	754	567	15	316	131	10	875	1071	39
16	905	672	11	561	342	48	757	609	6	637	451	65
All	728	757	779	551	528	691	336	220	416	577	610	1885

[1]NQ = location quality index

Table 5. Summary of average location error by location of transmission for 16 wolf PTTs in northwest Alaska during 1988 through 1991.

	Quality of Relocations											
	NQ1			NQ2			NQ3			All		
Location	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Selawik Cabin	967	962	290	618	584	408	414	258	188	689	719	886
Pick River	642	582	16	576	419	26	327	213	26	496	421	68
Kotzebue	907	1102	21	1049	899	15	372	303	8	858	949	44
Shungnak	333	163	5	683	382	9	267	123	2	522	349	16
Rabbit Mtn.	373	272	94	288	139	22	269	140	5	353	250	121
Kateel River	576	538	268	359	242	198	259	137	187	420	400	653
Kiliovilik	781	580	84	1097	749	13				824	611	97
All	728	757	779	551	528	691	336	220	416	577	610	1885

Table 6. Number of relocations by location quality index (NQ) by platform transmitter terminal (PTT) and odds ratios that NQ=1 and NQ=3 when PTT was on or off a wolf in northwest Alaska during 1988 through 1991.

	PTT on a wolf			PTT not on a wolf			Odds that NQ=1 on wolf vs. off		Odds that NQ=3 on wolf vs. off	
PTT No.	NQ1	NQ2	NQ3	NQ1	NQ2	NQ3	Ratio	P-VALUE	Ratio	P-VALUE
7909	188	85	3	18	57	20	8.923	<0.001	0.047	<0.001
7909a	41	32	0	16	26	74	7.778	<0.001	0.003	<0.001
7910a	70	25	0	13	14	4	3.789	0.001	0.031	<0.001
7911	220	42	1	17	14	6	5.938	<0.001	0.027	<0.001
7912	124	12	2	0	11	7	317.690	<0.001	0.028	<0.001
7912a	47	11	2	29	34	14	5.785	<0.001	0.187	0.007
7913	102	33	3	9	10	4	4.286	0.001	0.111	0.001
7913a	30	4	0	39	34	23	9.866	<0.001	0.045	0.002
7914	107	18	2	1	2	3	19.228	<0.001	0.019	<0.001
7914a	41	24	0	99	51	23	1.268	0.414	0.048	0.002
10908	157	28	3	114	37	15	2.293	0.001	0.184	0.001
10909	37	14	0	282	202	191	3.602	<0.001	0.024	<0.001
10910	318	131	12	8	8	4	3.264	0.007	0.101	<0.001
10911	22	6	0	10	0	2	0.824	0.730	0.073	0.027
10912	100	20	1	7	9	4	8.414	<0.001	0.045	<0.001
10913	298	94	12	56	46	24	3.497	<0.001	0.133	<0.001
10914	207	83	1	24	33	12	4.560	<0.001	0.023	<0.001

Table 6. Continued.

	PTT on a wolf			PTT not on a wolf			Odds that NQ=1 on wolf vs. off		Odds that NQ=3 on wolf vs. off	
PTT No.	NQ1	NQ2	NQ3	NQ1	NQ2	NQ3	Ratio	P-VALUE	Ratio	P-VALUE
10915	209	31	2	29	36	19	11.765	<0.001	0.034	<0.001
10916	65	30	1	19	38	6	4.745	<0.001	0.138	0.011
10917	11	2	1	14	15	10	5.778	0.006	0.312	0.143
Chi-square: homogeneity of ratios							65.9	(P<0.01)	23.4	(P=0.22)
common odds ratio=1.0							343.9	(P<0.01)	217.8	(P<0.01)
Common odds ratio							5.259*		0.076	

* Common odds ratio of 5.259 is only an indicator because homogeneity of ratios was rejected.

Table 7. Summary of average directional bias of wolf PTTs by location and NQ category as determined from known locations in northwest Alaska during 1988 through 1991.

	NQ1		NQ2		NQ3	
Location	Mean Angle	n	Mean Angle	n	Mean Angle	n
Pick River	334*	32	328*	52	330*	52
Shungnak	277	5	222	9		
Kateel River	237*	266	224*	198	237*	187
Kiliovilik River	240*	85	225*	13		
Rabbit Mt.	237*	95	202*	22	223*	5
Selawik	195	288	211*	412	195*	188
Kotzebue	103	24	135*	19	94*	8
Nome	283*	268	223*	239	301*	104

* Significant directional bias ($P < 0.05$).

CHAPTER 4

MONITORING WOLF ACTIVITY BY SATELLITE

Abstract: Indices of activity were monitored for 23 gray wolves (Canis lupus) in northwestern Alaska during 1987-1991 with a mercury tip-switch and microprocessor in transmitters compatible with the Argos Data Collection and Location System (PTTs: Platform Transmitter Terminals). Wolves were more active during summer than winter. Activity indices in summer (May - September) were highest between 2200 and 0600 h. During winter wolves were most active between 0700 and 1600 h. Activity indices in winter increased and became more variable as temperatures decreased. Activity sensors in PTTs can systematically monitor activity of wolves in remote areas throughout the year, but calibration studies with captive wolves are needed to determine the optimum tip-switch orientation for discriminating among specific activities.

Use of satellites to monitor movements and activities of free-ranging wildlife has expanded rapidly since 1984. The Argos Data Collection and Location System was used by the U. S. Fish and Wildlife Service and the Alaska Department of Fish and Game during 1984-1990 to obtain >100,000 locations of caribou (Rangifer tarandus), polar bear (Ursus maritimus), muskoxen (Ovibos moschatus), and

several other terrestrial mammals (Fancy et al. 1988, 1989; Harris et al. 1990). Recent advances in transmitter miniaturization and power supplies allow use of satellites for smaller species (e.g., wolves [Canis lupus], geese [Branta canadensis]) under a wide range of study conditions.

In addition to providing animal location, sensors in the transmitters or PTTs (Platform Transmitter Terminals) can monitor activity, ambient temperature, and other information by satellite (Fancy et al. 1988; Harris et al. 1990). We report here on the first use of satellites to monitor ambient temperature and activity of wolves. Accuracy, precision and performance of wolf PTTs were described by Ballard et al. (1993). Data on wolf movement patterns and comparisons of satellite telemetry with conventional VHF telemetry will be presented elsewhere.

METHODS

Fancy et al. (1988) presented a detailed description of the Argos system and its potential applications to wildlife research and management. Briefly, Argos instruments on two polar-orbiting satellites pass over Alaska approximately 24 times daily, receive signals from PTTs in the UHF (ultra-high frequency) range, and relay data to ground stations in Alaska, Virginia and France. Data are processed at Service Argos' computer facility in Landover, Maryland, and are received monthly on computer tapes or diskettes. Results may also be obtained 3-8 h following an overpass with a telephone modem and computer access to the Argos computer (Fancy et al. 1988).

Beginning in April 1987, we deployed PTTs (Telonics, Inc., Mesa, Arizona; mention of trade names does not constitute endorsement by the U. S. government) weighing 1.2 kg on 23 wolves weighing 28.6-51.7 kg (Table 1). Each collar was equipped with a UHF transmitter and a conventional VHF radio transmitter that allowed wolves to be located from aircraft. Separate power supplies and antennas were used for each transmitter. Wolves were immobilized for collaring by darting from a helicopter (Ballard et al. 1982, 1991).

Each transmitter package cost approximately $3500; annual data processing expenses were ca. $1400 per PTT. To

extend battery life, PTTs were programmed to transmit once each minute during the same 6-h period on alternate days. Unlike previous Telonics PTTs that used three "D" size lithium batteries, prototype PTTs used three "C" size batteries. This smaller battery pack provided a theoretical life of 6 months based on 6 h of operation every 48 h at the anticipated ambient air temperatures. The electronics, antenna, and transmitted signal were similar to heavier transmitters that were tested on large mammals (Fancy et al. 1988, 1989; Harris et al. 1990).

Messages transmitted to the satellite contained both short-term (previous minute) and long-term (previous day) indices of wolf activity (Fancy et al. 1988). Six PTTs deployed in 1987 and 1988 also transmitted ambient temperature data, sensed by a thermistor in the PTT. The short-term activity index (range = 1-60) was a count of the number of seconds each minute that a mercury switch in the canister was activated. Higher counts presumably indicated greater activity. The long-term index was the sum of short-term counts for a 24-h period (maximum value = 86,400), and was intended to indicate mortality or daily activity.

PTTs deployed in 1987-1989 (n = 14) had mercury tip-switches oriented parallel to the wolf's spine with the anterior end angled -4° relative to the bottom of the PTT canister (Table 1). In 1990-1991, we deployed 9 PTTs with

the anterior end of the switch angled +5° relative to bottom of the canister in an attempt to provide better delineation between activities.

The number of short-term activity counts received during a satellite overpass ranged from 1 to 13 (mean = 6.5 ± 2.0 [SD]), depending on the geometry of the overpass and the location of the wolf. We calculated a mean short-term activity index for each overpass and used it to subsequently calculate mean activity indices for each wolf and season. We compared means by two-way analysis of variance with season and switch angle as main effects (SAS 1987). To obtain hourly activity indices, we pooled data for all wolves having PTTs with the same switch angle within each season. Statistical significance was evaluated at the 95% confidence interval.

RESULTS

Mean operation time (including days prior to deployment on the wolf and after the PTT was retrieved) for the 23 PTTs was 253 ± 79 (SE) days. This life span was 40% greater than their expected 180-day life. Five PTTs operated longer than 1 year, but five others failed within 100 days of deployment. The manufacturer cited premature battery failure as the primary reason for the short life of some PTTs.

As expected, mean short-term activity counts for PTTs with a -4° tip-switch angle were higher than those for PTTs with a +5° angle in both summer and winter ($F = 7.39$, $P = 0.011$). Activity counts were higher in summer than in winter for wolves wearing PTTs with either switch angle ($F = 13.54$, $P = 0.001$; Table 2). In summer, wolves appeared to be most active between 2200 and 0600 h AST (Alaska Standard Time) whereas in winter activity counts were highest between 0700 and 1600 h (Fig. 1).

Long-term (24-h) activity counts were 144% (switch angle = -4°) and 820% (switch angle = +5°) higher in summer than in winter. For most wolves, activity counts were not highly correlated with movement rates. Long-term activity counts correlated with daily movement rates for only 6 of 22 wolves in summer and 4 of 12 wolves in winter. Similarly, short-term activity counts correlated with movement rates

for only 5 of 22 wolves in summer and 2 of 12 wolves in winter.

Ambient temperatures transmitted by PTTs were within extremes recorded at nearby weather stations (Fig. 2). The wolf's winter temperatures were more variable than those in summer and frequently exceeded the maximum recorded temperature at Ambler. Behaviors such as curling the body to reduce heat loss, seeking relatively warm microenvironments, and basking on south-facing slopes may explain the greater variation in winter temperatures.

We found significant inverse correlations between temperature and both mean short-term activity counts and standard deviation of activity counts for 6 of 6 wolves in winter, but for only 1 of 6 in summer.

DISCUSSION

Activity and temperature data for wolves were collected incidental to our primary objective of obtaining seasonal movement and home range data for determining wolf numbers (Ballard et al. 1989). Activity patterns of wolves have previously been studied at den and rendezvous sites (e.g., Mech 1970; Harrington and Mech 1982; Ballard et al. 1992), but this is the first study to systematically obtain activity data for wolves throughout the year.

Wolves were more active in summer than in winter, and during summer were most active between 2200 and 0600 h. These findings agree with most previous studies of wolf activity (e.g., Kelenosky and Johnston 1967; Mech 1970; Ballard et al. 1992). Mech (1970) and Harrington and Mech (1982) thought the usual pattern of daytime attendance and nighttime absence of wolves from homesites was related to the wolf's inability to tolerate high summer temperatures, particularly in tundra areas where they cannot escape the heat because of lack of cover. Our finding that in winter wolves were most active during the limited daylight hours between 0700 and 1600 h support this hypothesis.

The mercury tip-switches and software used to obtain activity counts may provide better discrimination among wolf activities than variable-pulse activity transmitters used by Gillingham and Bunnell (1985) and Beier and McCullough

(1988), but calibration studies with captive wolves are needed (Kunkel et al. 1991). Fancy et al. (1988) found a high correlation between the short-term activity index and specific activities (e.g., lying, feeding, walking), and between the 24-h activity index and daily movement rates for caribou, but several switch angles and counting intervals were tried with captive caribou before the best configuration for discriminating among activities was determined. Kunkel et al. (1991), using Wildlink collars (Wildlink, Inc., Brooklyn Park, MN 55444), were able to discriminate among three activity levels for captive wolves. Similar to the activity sensor used in Telonics PTTs, Wildlink collars contain a microprocessor that records the number of tip-switch activations within a programmed time interval and stores the counts for later transmission.

We deployed PTTs with two switch angles on wild wolves, but lacked detailed observations needed to calibrate activity counts with specific wolf activities. The +5° tip-switch angle required greater movements of the wolf's neck to activate the switch and therefore produced lower counts than the -4° angle, but neither angle produced counts that correlated with movement rates. Activity counts for wolves from PTTs appear to be useful as gross indices of wolf activity, but calibration studies with captive wolves are

needed to determine the best switch orientation for discriminating among specific activities.

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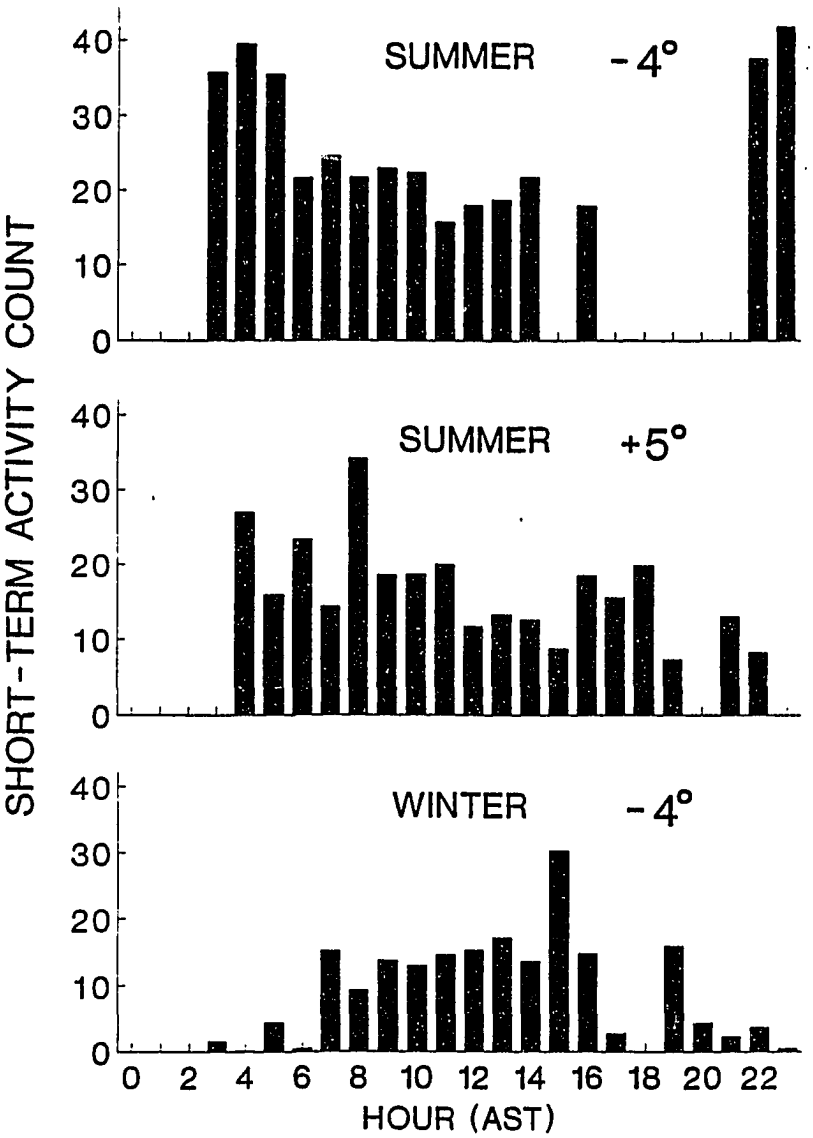


Fig. 1. Mean hourly activity counts for 23 Gray Wolves in summer (May - September) and winter (October - April), northwestern Alaska, 1987 - 1991. The anterior end of mercury tip-switches in satellite transmitters were oriented -4° (n = 13, summer; n - 10, winter) or +5° (n = 9, summer) relative to the bottom of the canister.

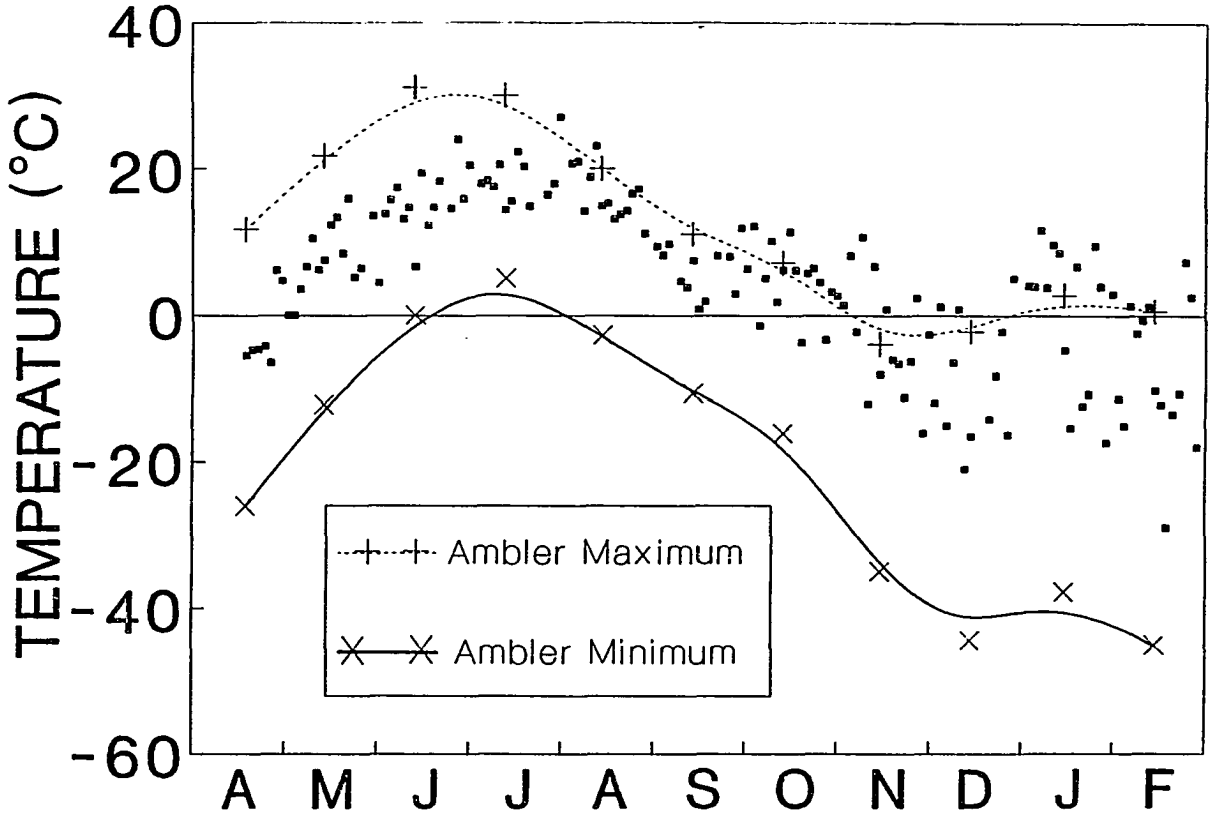


Fig. 2. Temperatures recorded by a sensor in a PTT (Platform Transmitter Terminal) deployed on a wolf in northwestern Alaska. Monthly extreme temperatures (minimum and maximum) recorded at Ambler, Alaska, are shown.

Table 1. Transmission dates and mercury tip-switch angles for satellite radio collars while deployed on wolves in northwest Alaska, 1987-1991.

Trans-mitter No.	Wolf no.	Pack	Sex	(kg)	Angle	Collar on Wolf Dates	No. days
7900	001	Rabbit Mt	M	43.2	-4°	17 Apr 87 29 Feb 88	319
7909	007	Jade Mt	F	37.6	-4°	25 Apr 88- 21 Feb 89	303
7909	067	Pick Rv	F	39.0	+5°	14 Apr 90- 28 Jun 90	76
7910	016	Ingruksukruk	F	28.6	-4°	26 Apr 88- 13 Aug 88	110
7910	037	Pick Rv	F	44.9	-4°	15 Apr 89- 11 Jul 89	88
7911	012	Purcell Mt	F	33.1	-4°	13 Jun 88- 19 Apr 89	311
7912	010	Nuna Ck	F	47.6	-4°	28 Apr 88- 06 Mar 89	313
7912	072	Upper Tag	F	39.0	+5°	17 Apr 90- 17 Jun 90	62
7913	024	Pick Rv	M	47.6	-4°	16 Nov 88- 18 Feb 89	95
7913	074	Ingruksukruk	M	49.4	+5°	17 Apr 90- 05 Jun 90	50
7914	014	Rabbit Mt	F	44.9	-4°	26 Apr 88- 16 Feb 89	297
7914	032	Kiliovilik	F	36.7	+5°	18 Apr 90- 11 Jun 90	55
10908	030	Rabbit Mt	F	37.2	-4°	10 Apr 89- 03 Jan 90	269
10909	048	Kateel Rv	M	51.7	-4°	14 Apr 89- 25 Jun 89	73
10910	033	Dunes	F	47.2	-4°	10 Apr 89- 01 Feb 90	298
10911	002	Purcell Mt	F	45.4	-4°	14 Apr 89- 07 Aug 89	116
10912	040	Ingruksukruk	F	34.5	-4°	14 Apr 89- 19 Oct 89	188
10913	046	Upper Tag	F	38.1	-4°	14 Apr 89- 14 Apr 90	366

Transmitter No.	Wolf no.	Pack	Sex	(kg)	Angle	Collar on Wolf	
						Dates	No. days
10914	033	Dunes	F	47.2	+5°	18 Apr 90- 27 Feb 91	316
10915	064	Purcell Mt	F	39.9	+5°	18 Apr 90- 01 Dec 90	228
10916	057	Salmon Rv	F	50.8	+5°	14 Apr 90- 21 Jul 90	99
10917	055	Nuna Ck	F	46.7	+5°	14 Apr 90- 05 Jun 90	53
10918	050	Kiliovilik	M	40.4	+5°	14 Apr 90- 03 Jun 90	51

Table 2. Short-term activity counts for wolves wearing PTTs (Platform Transmitter Terminals) with the anterior end of the mercury tip-switch angles -4° and +5° relative to the bottom of the PTT canister.

Switch Angle	Season	n	Mean	SE
-4°	Summer	12	22.28	2.55
	Winter	9	12.27	1.38
+5°	Summer	9	15.33	1.38
	Winter	2	1.91	0.29

CHAPTER 5

COMPARISON OF TWO METHODS TO AGE GRAY WOLF (Canis lupus) TEETH

ABSTRACT: We compared the Harris' modified hematoxylin stain (HMH) with the Giemsa stain (GS) for aging wolf (Canis lupus) canine and first premolar teeth. Ages derived from canine teeth for the two stains were not significantly different ($P = 1.00$). Premolar teeth stained with the HMH stain could not be accurately aged, but those stained with the GS stain provided ages that were not significantly different ($P = 0.43$) from those provided by canines with the HMH. Based on our results, wolf premolars stained by the GS method and canine teeth stained with the HMH method appear to provide similar ages, suggesting that premolar teeth extracted from live wolves can be used to estimate age by the less expensive GS method. However, further testing using known-age specimens is needed.

INTRODUCTION

Obtaining accurate and precise age estimates of gray wolves (Canis lupus) has been difficult. Gray wolves have been aged by tooth wear and replacement (Van Ballenberghe et al. 1975, Fuller and Keith 1980, Fritts and Mech 1981, Ballard et al. 1987), examination of epiphyseal cartilage of long bones (Rausch 1967), counts of cementum annuli (Goodwin and Ballard 1985), and dentine width and root closure (Parker and Maxwell 1986). Tooth wear and replacement can be unreliable, particularly beyond the pup and yearling age classes because factors other than age may cause wear variation. Also, aging by tooth wear is subjective and depends upon the experience of the estimator. Examination of long bones allows wolves to be placed into pup or adult age classes, but with unknown accuracy and precision. Similarly, root closure and dentine width only allows identification of pup and yearling age classes.

Counts of cementum annuli from teeth that have been sectioned and stained provide the most accurate and precise estimates of ages from most wildlife species (Grue and Jensen 1979, Fancy 1980). This method was reported useful with wolves, based on known-age specimens by Goodwin and Ballard (1985). They used the Harris' modified hematoxylin stain (Cable 1958) with hot bath (HMH). Although the method provided relatively accurate age estimates, it was only

useful on canine teeth and thus was not practical for use on live wolves. E. A. Goodwin (Alas. Dep. Fish and Game, unpubl. data) and W. B. Ballard (unpubl. data) attempted to stain first premolar teeth using the same method successfully used on canine teeth but could not consistently identify cementum annuli. They concluded that further research was needed on the suitability of using incisors and premolars for aging.

Since the late 1970s biologists from Alaska, Northwest Territories, and Yukon Territory (G. Matson, Matson's Laboratory, Mont., pers. commun.) have pulled premolar teeth from live wolves for determining age. The Giemsa stain (GS) (Schneider 1973, Stone et al. 1975) has been widely used (n = 2,481 wolves from Alaska and Canada [unpubl. data]) because teeth can be commercially processed at relatively low cost. However, the Giemsa stain and aging method has not been adequately evaluated with known-age specimens nor has it been compared with other methods. Ideally the method should be tested with known-age specimens, but these are difficult to obtain. Goodwin and Ballard (1985) used known-age specimens for validation of the HMH method. We wanted to examine the GS staining method but lacked known-age specimens for adequate evaluation. Consequently, we compared the two staining and aging methods using many of the specimens aged by Goodwin and Ballard (1985). Since

their method was developed based on known-age material, we assumed that the HMH ages using canine teeth were accurate and used them as baseline values.

Our objectives in this study were to: (1) compare estimated ages obtained from counting cementum annuli in wolf canine teeth using the Harris' modified hematoxylin stain with hotbath to those obtained by staining with Giemsa stain (Schneider 1973, Stone et al. 1975) using a standardized aging model (G. M. Matson, unpubl. data); (2) test GS on premolar teeth from wolves aged by Goodwin and Ballard (1985) using HMH; (3) compare ages obtained between canine and premolar teeth using the GS method; and (4) provide a model for aging wolf canine and premolar teeth to standardize methods for aging gray wolves.

METHODS

Procedures for cutting, staining, and estimating the age of wolf canine and premolar teeth using HMH method were described by Goodwin and Ballard (1985); procedures used for the GS method were described by Schneider (1973), Stone et al. (1975), and Matson (1981). All specimens were obtained from wolves harvested in south-central Alaska. A wolf birthdate of 1 May (Ballard et al. 1992) was used for aging purposes. Goodwin and Ballard (1985) determined canine cementum age by identifying the first well-developed dark annulus as the age indicator for 2-year-olds. Their model was similar to that described by Linhart and Knowlton (1967) for aging coyote canines (Canis latrans). Matson (1981) determined both canine and premolar cementum ages based on a poorly defined but often present first annulus in 1-year-old wolves. The latter model was similar to that described for coyote canines by Allen and Kohn (1976). Evidence from both wolf canine and first premolar tooth sections indicates that the dark cementum annulus first becomes visible at the extreme periphery of canine and premolar teeth collected in March and April. The addition of 1 year to the dark annulus count in teeth collected during late winter provides the age to the nearest full year.

Cementum ages of canine teeth previously aged by Goodwin and Ballard (1985) were compared with ages obtained using the GS method based on canines extracted from the same wolves. One or two first premolars were extracted from each wolf skull, stained and aged by the GS method, and then ages were compared with those obtained from the canines using the HMH and GS methods. Teeth that were severely altered in histology because of resorption, heat exposure, or breakage were excluded from analyses. Ages for different teeth from the same wolf were assigned without knowledge of prior results. Comparisons among tooth-stain methods were compared by Wilcoxon matched pairs tests (Ott 1988).

RESULTS AND DISCUSSION

Wolf ages estimated from canine teeth (n = 22) using the HMH and GS method were not significantly different (Z = 0.0, P = 1.00). All of the GS ages were within 1 year of the estimates provided by the HMH method (Table 1). Both methods of staining and annulus counting provide similar age estimates for canine teeth.

There were no significant differences (Z = 0.79, P = 0.43) between HMH canine ages and premolars stained by the GS methods. Forty-eight percent of the GS ages (n = 67) were identical to the ages provided by the HMH method and 87% within $\pm$1 year of the HMH age (Table 2). There was a slight tendency for older animals (> 6 years) to be underaged by 1-2 years with premolars. Ages estimated from premolars using the GS method were significantly lower (Z = 1.98, P = 0.048) than GS canine ages (Table 3). These differences suggest there are unidentified sources of error in the aging models for one or both tooth types. Canine teeth sections have thicker cementum layers than premolars, and greater separation between annuli permits the complex repeated annual patterns to be more easily identified. The illustrated description of the aging method for canines (Fig. 1) and premolars (Fig. 2) provides a reference that helps insure consistency of annulus interpretation. The complete reference standard or "model" defines the criteria

for annulus identification and identifies the season during which the annulus was formed.

Goodwin and Ballard's (1985) known-age sample was largely composed of pup and yearling age classes (86% of 63 samples). Consequently both the HMH and the GS methods are in need of validation with a larger sample size of older age classes. Based on our results, wolf premolars stained by the GS method and canine teeth stained with the HMH method appear to provide similar ages. Perhaps more importantly, premolar teeth can be extracted from live wolves and aged by the GS method.

Use of the GS method for aging canine and premolar wolf teeth has two distinct advantages over the HMH method described by Goodwin and Ballard (1985): (1) the GS method has been successfully used on premolar teeth, and (2) the GS method is considerably cheaper to use. The HMH method was labor intensive (25 teeth processed per day) and currently cost approximately $10.55/tooth (E. A. Goodwin, Alas. Dep. Fish and Game, unpubl. data). Because of the high costs and intensive labor, large numbers of teeth could not be processed on a routine basis. In contrast, the GS method currently costs about $2.85/tooth and commercial processing is available. The latter service also includes a subjective estimate of the variance associated with each cementum age.

The tooth cementum method, though useful, is in need of more evaluation and testing. The development of an accurate and precise method of cutting, staining, counting cementum annuli, and estimating ages of wolf teeth has been inadequately evaluated because of an insufficient number of known-age samples from several age classes. There is a strong need for wolf biologists to pool their known-age specimens so that aging methods can be appropriately tested and refined. A number of questions remain concerning the deposition of annuli and their interpretation. Goodwin and Ballard (1985) estimated that the first annulus was deposited between 18 and 22 months-of-age in canine teeth, but the assessment was based on four wolves. Using different criteria a "juvenile" annulus, formed before 1 year of age, and a 1-year annulus can be identified in known-age teeth (Figs. 1 and 2). We need to determine if there are differences in the timing and extent of annulus deposition in different teeth and in wolves from different regions.

Use of the GS method for processing wolf premolar teeth has potential for estimating ages of free-ranging wolves but requires further testing with known-age specimens. Accuracy can be further improved by using only experienced personnel and a combination of root closure, examination of longbones,

and tooth eruption and wear along with the estimates provided by cementum annuli.

Acknowledgements

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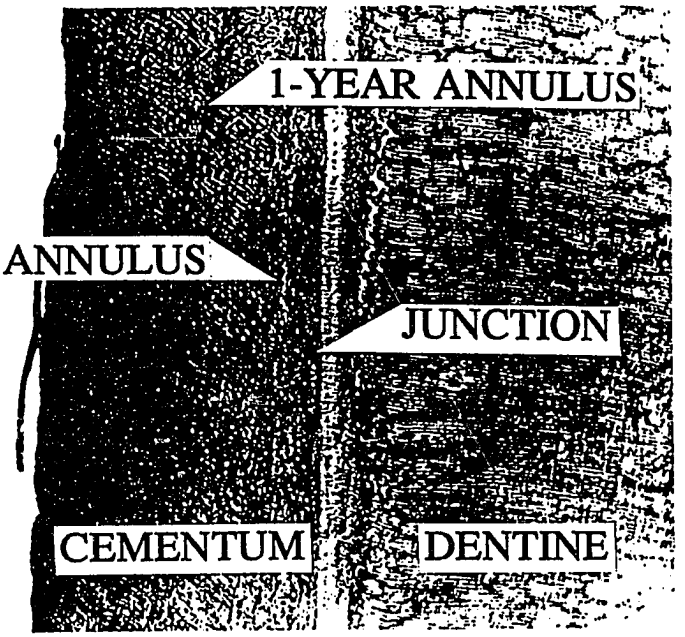
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Fig. 1. Wolf canine mid-sagittal sections. 60X. A. Wolf No. 122062. 5 mm above root tip. Known-age = 22 months. Tooth collected on 21 March. B. Wolf No. 122179. 2 mm above root tip. 60X. Not known age. Cementum age = 4 years. Tooth collected on 31 December. A "juvenile annulus (JA) may be formed before the age of 1 year. It is differentiated from the 1-year annulus by two characteristics: (1) it is present at the root tip, as the first identifiable annulus distal to the dentine, but is absent above the root tip, and (2) it is simple with only a single component and stains indistinctly. The 1-year annulus is present both at the root tip and above it, and stains less distinctly than the 2-year annulus. The first prominent annulus is the 2-year annulus. Annuli formed during subsequent years are similar to the 2-year annulus in staining intensity and characteristics. All annuli may be complex, having more than a single component. Light cementum is produced in gradually lessening amounts, with the greatest production occurring during the first summer and autumn of life. The dark annuli appear to be formed during winter, and first become visible in late March or April just before the assumed 1 May birthday. To determine the age of summer-autumn-winter collected teeth, each dark annulus is counted as 1 year. To determine the age of spring-collected teeth the last formed annulus is not

counted as a year of age of until after the assumed birthday of 1 May. Fractions of the year may be added to the annulus count according to the month of tooth collection.

A


1-YEAR ANNULUS
JUVENILE ANNULUS
JUNCTION
CEMENTUM
DENTINE

B

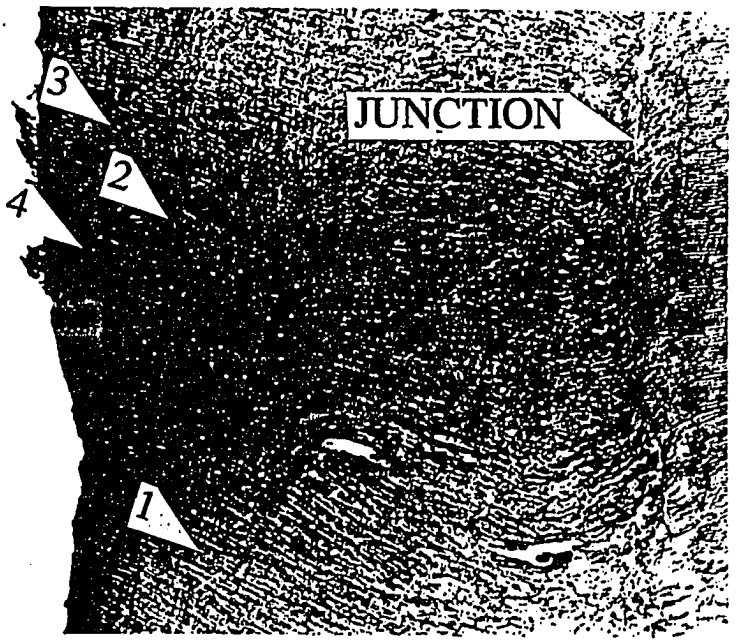
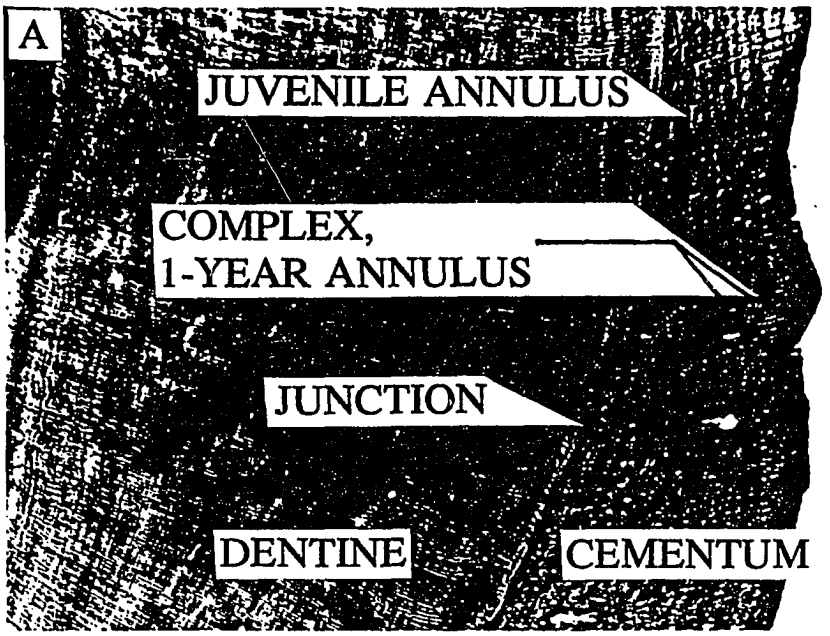

3
JUNCTION
2
4
1

Fig. 2. Wolf premolar 1 (PM1) mid-sagittal sections. 60X. A. Wolf No. 122062. 2mm above root tip. Known-age = 22 months. Tooth collected on 21 March. B. Wolf No. 122179. 2mm above root tip. 60X. Not known aged. Cementum age = 4 years. Tooth collected on 31 December. This aging model is similar to that of the canine tooth but differences exist because the smaller size of the premolar compresses annuli closely together making identification of annuli difficult. Complex annuli are sources of cementum aging error in canine and premolar teeth. There are two criteria for differentiating the complex annulus from its non-annual components: (1) the major annulus component is uniformly present at most points of the tooth section; and (2) complex annuli are uniformly spaced at regularly diminishing distances during successive years.


A
JUVENILE ANNULUS
COMPLEX,
1-YEAR ANNULUS
JUNCTION
DENTINE
CEMENTUM

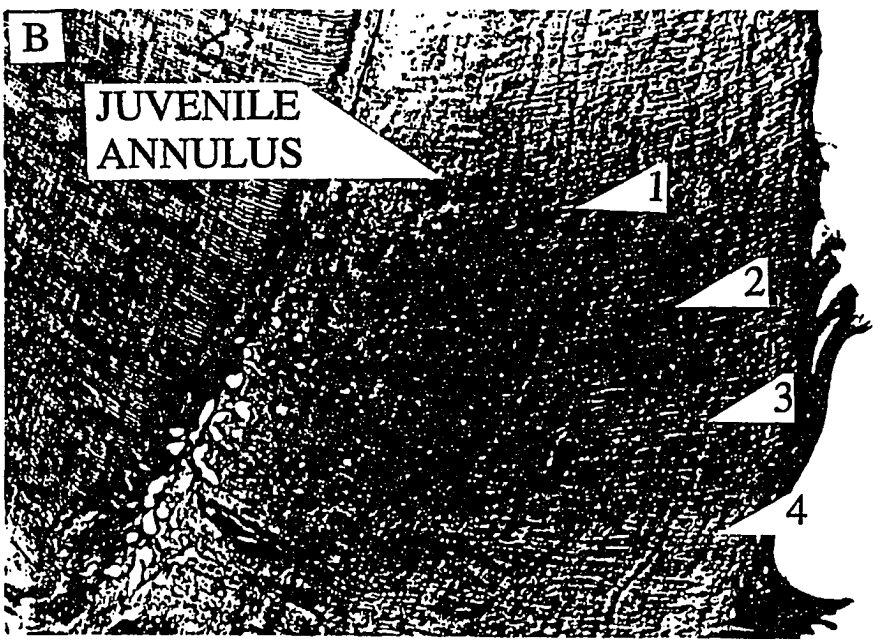

B
JUVENILE
ANNULUS
1
2
3
4

Table 1. Deviation of ages of wolf canine teeth using the Giemsa stain method (GS) and the Harris' modified hematoxylin stain with hotbath method (HMH).

	Deviation from HMH canine ages (yrs)		
HMH Age	-1	0	+1
1		2	
2	1	2	1
3	2	4	1
4		1	3
5		1	
6	2		
7			
8	1		
9			
10			1
Totals	6	10	6

Table 2. Deviation of wolf premolar teeth ages using Giemsa staining method (GS) from those provided by canine teeth using Harris' modified hematoxylin stain with hotbath method (HMH).

	Deviation from HMH canine ages (yrs)								
HMH Age	-4	-3	-2	-1	0	+1	+2	+3	+4
1					4	3			
2				3	7	3	2		
3			3	5	8	2			
4				1	8	4	1		
5					4	1			
6			1	4	1				
7									
8	1		1						
Totals	1	0	5	13	32	13	3	0	0

Table 3. Deviations of ages of wolf premolar and canine teeth using the Giemsa staining method (GS).

GS Canine Age	Deviation from GS canine ages (yrs)						
	-3	-2	-1	0	+1	+2	+3
1				1			
2			1	3	1	1	
3			2	7			
4		1		2			
5		1	2	6	1		
6							
7	2		2				
Totals	2	2	7	19	2	1	0

CHAPTER 6

IMMOBILIZATION OF GRAY WOLVES WITH A COMBINATION OF TILETAMINE HYDROCHLORIDE AND ZOLAZEPAM HYDROCHLORIDE

ABSTRACT: We immobilized 51 free-ranging gray wolves (Canis lupus) with a combination of tiletamine hydrochloride and zolazepam hydrochloride. Effective initial dose was 400 mg ($\bar{x}$ = 10.4 ± 0.6 [SE] mg/kg of body mass. Mean induction and recovery times were 7.2 ± 1.4 minutes and 144 ± 35 minutes, respectively. We did not observe adverse effects.

J. WILDL. MANAGE. 00(0):000-000

Key words: Canis lupus, immobilization, tiletamine hydrochloride, wolves, zolazepam hydrochloride.

Phencyclidine hydrochloride, etorphine hydrochloride, and ketamine hydrochloride have been used to immobilize free-ranging gray wolves captured in traps or darted from helicopters (Seal et al. 1970; Mech 1974; Ballard et al. 1982, 1987; Fuller and Kuehn 1983). Other drugs should be tested (Carbyn 1987) because phencyclidine is no longer commercially available, etorphine is relatively expensive (approx $95/20 mL) and extremely toxic to humans, and ketamine alone or in combination with xylazine or promazine has resulted in cardiac abnormalities and prolonged induction times (Fuller and Kuehn 1983; W. P. Taylor, Alas.

Dep. Fish and Game, pers. commun.). A combination of tiletamine hydrochloride and zolazepam hydrochloride (Telazol, A. H. Robins Co., Richmond, Va.) has been successfully used on free-ranging polar bears, black bears (U. americanus), and grizzly bears (Haigh et al. 1985, Stewart et al. 1980, Taylor et al. 1989) with relatively low rates (<1%) of capture mortality. Telazol has also been successfully used to immobilize captive gray wolves (Boever et al. 1977, Schobert 1987), but its effectiveness for immobilizing free-ranging wolves has not been reported.

Boever et al. (1977), Schobert (1987), and Taylor et al. (1989) describe the pharmacology of Telazol. Tiletamine hydrochloride alone produces cataleptoid anesthesia that may be accompanied by convulsive seizures (Boever et al. 1977). Zolazepam hydrochloride is a nonphenothiazine diazepinone tranquilizer that when used alone can cause belligerency (Boever et al. 1977). The undesirable characteristics of each drug individually are eliminated when the drugs are combined. Tiletamine hydrochloride and zolazepam hydrochloride anesthesia is characterized by retention of cranial, spinal, laryngeal, and pharyngeal reflexes. Eyes usually remain open. We established effective dosages of Telazol for immobilizing free-ranging gray wolves darted from helicopter.

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STUDY AREA

We conducted this study in and adjacent to the Selawik National Wildlife Refuge and Kobuk Valley National Park, Alaska. The Baird and Purcell Mountains occur along the northern and southern boundaries of the study area, respectively. The Waring Mountains divide the study area into the Kobuk River drainage to the north and the Selawik River drainage to the south. Much of the area is underlain by permafrost and has numerous shallow ponds and lakes. Climate is characterized by temperatures ranging from -23 C in winter to 32 C in summer (USFWS 1987). Annual precipitation ranges from 38-50 cm in lowland areas to 76 cm in mountainous areas. Elevations range from about 33 m along the major drainages to >1,100 m in the Baird Mountains. Vegetation types are varied but consist primarily of tundra and taiga. Short sparse stands of black spruce (Picea merino) and white spruce (P. glauca) occur throughout the study area, but thick forests are often restricted to narrow bands along major river systems.

METHODS

We located wolves after a fresh snowfall by searching edges of streams and lakes or ridgelines for footprints from Piper PA-18 fixed-wing aircraft or by radio tracking previously marked packs. We routinely captured wolves during the months of November and April when snow depths were >8 cm, usually between 0800 and 1800 hours with ambient air temperatures ranging from -23 C to 0 C. Capture efforts during other months were opportunistic. Once wolves were spotted from fixed-wing aircraft, their locations were relayed via radio to a nearby Bell 206B helicopter. We used the methods described by Ballard et al. (1982) and darted wolves (Chap-Chur gun, Palmer Chemical Co., Douglasville, Ga.) with a 3-cc dart fired from the helicopter. Approximately 1-5 minutes passed from the time a wolf was spotted from the helicopter until it was darted. The helicopter withdrew several hundred meters to monitor the darted animal or landed >1 km away while the animal was monitored from fixed-wing aircraft. Up to 5 members per pack were immobilized each trip.

Powdered Telazol in 500-mg vials was reconstituted with sterile water to yield a 200 mg/mL concentration. Because wolves cannot be aged accurately from fixed-wing aircraft, a safe dosage for both pups and adults was needed. Grizzly bears (Ursus arctos) (Taylor et al. 1989) and wolves (P.

Clarkson, Gov. Northwest Territ., pers. commun.) were immobilized with approximately 9 mg/kg, so we used 400 mg initially. This dose allowed use of 3-cc darts for all wolves. As soon as was practical after immobilization, we regularly monitored wolves' rectal temperature and respiration (breaths/min).

Induction time was defined as the period beginning when an animal was struck by a dart to the point when it was immobilized enough to allow safe approach and handling. Recovery time was defined as the period from immobilization to the time the animal departed the area or no longer exhibited drug influence in gait and head movements. We used Mann-Whitney U-tests to compare differences among means. Statistical significance was assumed when $P < 0.05$ unless stated otherwise.

RESULTS

We immobilized 51 free-ranging wolves (30 F, 20 M, and 1 unknown sex) from ages 3 months to 9 years with Telazol during late autumn, spring, and summer 1988-89 (Table 1). Forty-eight wolves were immobilized with an initial dose of 400 mg ($\bar{x}$ = 10.41 $\pm$ 0.61 mg/kg). Induction time averaged 7.2 $\pm$ 1.4 minutes. We administered additional drug to 3 wolves after the initial injection. Of those three, one was accidentally double-dosed (17.3 mg/kg), one was given an additional 200 mg within 8 minutes after the initial injection (12.7 mg/kg), and one 3-month-old female (11.3 kg) initially dosed with 200 mg required an additional 200 mg (35.4 mg/kg) 29 minutes after the first injection. Induction times for these 3 wolves were 0.7, 10.0, and 32.0 minutes, respectively. Immobilized wolves were safely handled an average of 70 minutes. After that time period, additional drug was sometimes required if further examination is necessary. Recovery time averaged 144 minutes, ranging from 26 to 301 minutes (Table 1).

Because darts often fall out before immobilization, the frequency of incomplete injections due to malfunctioning darts could not be evaluated. Cost/dose was $6.22 excluding missed shots. A mean of 3 shots/wolf was required for a successful hit.

Induction times of females and males of all ages (excluding 1 11.3-kg pup) were not significantly different ($P = 0.29$) even though females were lighter ($P < 0.05$) and, consequently, had higher ($P = 0.001$) doses per kilogram of body mass than males (Table 1). Female dosages ranged from 8.3 to 20.0 mg/kg, excluding 1 pup (11.3 kg) that received 35.4 mg/kg. Dosage rates for males ranged from 7.7 to 12.6 mg/kg. Adults of both sexes had longer induction periods ($P < 0.05$) than pups within a season. These differences were related to larger body mass and smaller doses per kilogram of body mass. Induction times and specific dosages for 2 adults immobilized during June were within the range of values for adults immobilized during April and November. Behavioral characteristics of immobilization were similar to those described for polar bears (Ursus maritimus) and grizzly bears (Haigh et al. 1985, Taylor et al. 1989), except high stepping was often the first recognizable response followed by disoriented gait, loss of use of hindlegs, licking lips, loss of use of forelegs, loss of head and neck movement, nystagmus, and loss of tongue movement. Extreme salivation occurred in 4 cases.

Rectal body temperatures after immobilization were moderately elevated (Table 1) but declined to normal levels (38.6 C) within approximately 75 minutes after induction. There were no differences ($P < 0.05$) in initial mean

temperatures by sex or age class. Respiration (breaths/min) after immobilization exhibited a similar pattern, initially averaging 35.6 breaths per minute but declining quickly. Other than mild seizures in 3 wolves no adverse effects were observed following induction. The safety of Telazol for pregnant animals has not been established but 6 of 13 adult females immobilized during spring were pregnant and successfully gave birth; females and young were alive for at least 8 months after induction until killed by hunters.

DISCUSSION

A mixture of tiletamine hydrochloride and zolazepam hydrochloride has advantages over other drug combinations used to immobilize free-ranging wolves. These include its low cost, lower human toxicity (U.S. Fed. Drug Admin. Class III drug), and relatively rapid induction times. Although Telazol does not have an antagonist, respiration rates in domestic dogs have been increased and arousal times shortened with administration of doxapram hydrochloride (Dopram-V, A. H. Robins Co., Richmond, Va.) (Schobert 1987). We recommend an initial dose of 400 mg for immobilizing all wolves $\geq$ 6 months old when darting from helicopter during autumn or spring. Pups < 6 months old should be dosed at about 10.0 mg/kg of body mass. Smaller doses should probably be used if wolves are not darted from helicopter.

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Table 1. Statistics associated with capture and handling of gray wolves immobilized with a mixture of tiletamine hydrochloride and zolazepan hydrochloride in northwest Alaska, 1988-89.

		Mass (kg)		Drug dosage (mg/kg)		Induction time (min)		
	n	X	SE	X	SE	X	SE	Range
Ad F	14	41.8	1.34	9.70	0.322	8.1	1.79	2.0-23.0
Pup F[a]	15	35.9	1.46	11.68	0.732	7.2	4.23	1.0-62.0
F Combined	29	38.7	1.13	10.73	0.446	7.62	2.25	1.0-62.0
Adult M	17	47.4	0.70	8.46	0.128	5.6	1.01	0.7-18.0
Pup M	3	39.9	4.47	10.29	1.210	4.7	0.88	3.0-6.0
M Combined	20	46.3	1.02	8.73	0.239	5.5	0.86	0.7-18.0
Total	50[b]	41.3	1.13	10.41	0.612	7.2	1.40	0.7-62.0

Table 1. Continued.

		Body temperature (C)			Recovery time (min.)		
	n	X	SE	Range	X	SE	Range
Ad F	14	39.6	0.26	38.5-41.1	117.5	46.7	26-214
Pup F[a]	15	39.6	0.24	38.1-41.3	186.6	55.1	41-301
F Combined	29	39.5	0.19	37.2-41.3	155.9	36.8	26-301
Adult M	17	39.6	0.26	37.6-41.3	40.0	0.0	
Pup M	3	39.4	0.19	39.4-40.1			
M Combined	20	39.7	0.22	37.6-41.3	40.0	0.0	
Total	50[b]	39.6	0.14	37.2-41.3	144.3	34.9	26-301

[a]Not included in totals.

[b]Includes 1 wolf of unknown sex and age.

CHAPTER 7

SUMMARY

Telazol rapidly immobilizes wolves which have been darted from helicopter. Prior to this study, biologists used etorphine hydrochloride (M-99) for immobilizing wolves. They had previously used phencyclindine hydrochloride (Sernylan), which was no longer commercially available due to narcotics restrictions imposed by the Federal government. Although M-99 was a useful drug, it was expensive (i.e., >$100 per 20 ml vial) and extremely toxic to humans. Consequently we searched for alternative drugs. Our study demonstrated that Telazol was relatively inexpensive (i.e., <$10/vial), produced relatively rapid induction with minimal side effects, had a predictable recovery pattern, and was substantially less toxic to humans than was M-99. As a result of our study, Telazol has now become the drug of choice for wolf immobilization and is now used throughout Alaska and Canada.

Prior to this study the only validated aging technique using tooth cementum annuli was provided for canine teeth by Goodwin and Ballard (1985). Major disadvantages of the Goodwin and Ballard method were it could only be used on dead animals and it was relatively expensive (approximately $11/tooth). Biologists have recently extracted premolar teeth from living animals and used these teeth to establish

ages. However, aging accuracy for these teeth is unknown, and they had been sectioned and stained with an untested method (Giemsa stain). We compared the ages on canine teeth aged by the Goodwin and Ballard (1985) method with those on canine and premolar teeth from the same wolves stained and aged by the Giemsa staining method. Results indicated that there were good correlations in ages obtained with the two staining and aging methods. Our results, although by no means conclusive, suggest that relatively reliable ages can be obtained by using premolar teeth extracted from live wolves. Major advantages of the new method are that live wolves can be aged at relatively low cost (<$3/tooth). Problems still exist (i.e., exact age at which first annulus is deposited has not been thoroughly investigated), but cementum aging is probably superior to aging wolves with subjective methods such as tooth wear and replacement. Research on wolf aging methods has been hampered by lack of adequate numbers of known-aged specimens which could be rectified if wolf researchers would pool known-age specimens. Further research into refinement of wolf aging methods is required before wolves can be accurately aged.

All methods historically used to estimate wolf abundance in North America suffer from a number of inadequacies. None of the methods provide an estimate of precision, and the accuracy of all methods is unknown. We

reported on the use of a statistical procedure employing line-intercept track sampling and compared this method with others used in North America and, in particular, those historically used in Alaska. We found that the line-intercept track sampling procedure (referred to as a TIP survey) provided a relatively accurate estimate of wolf abundance within an area of known wolf abundance. The TIP survey estimate for a 5,011 km^2 study area in northwest Alaska was 50.7 wolves and the known number was 48. The statistical 80% confidence interval was 33 to 68 but the biological interval was 43 to 68. Although the method has low precision, it is the only method that provides an associated estimate of precision. We also compared a TIP survey estimate with an estimate provided by a non-systematic method of counting wolves and wolf tracks (referred to as the Stephenson [1978] method) and found that the two point estimates were relatively similar (33 versus 36 wolves, respectively). One major advantage of the TIP survey method over other methods is that it is a sampling procedure rather than a total count. Other advantages include objectivity, repeatability, speed, reduced cost, reasonable accuracy, and measurable precision. We concluded that, in areas where biologists need a measure of precision with wolf population estimates, the TIP procedure offered a cost effective opportunity for obtaining such estimates.

Further research is necessary to increase the precision of the point estimate.

Prior to this study, satellite telemetry had been used on several relatively large mammalian species (i.e., caribou [Rangifer tarandus]), polar and grizzly bears [Ursus maritimus and U. arctos], moose [Alces alces], muskoxen [Ovibos moschatus], Pacific walrus [Odobenus rosmarus divergens], Dall sheep [Ovis dalli], elk [Cervus elaphus], and mule deer [Odocoileus hemionus] (-Fancy et al. 1988, Harris et al. 1990, and Ballard et al. 1993). However, our study was the first to employ satellite technology on a relatively small mammal such as wolves (70-100 kg). During 1987 through 1991, we deployed 23 satellite transmitters on wolves of both sexes ranging in age from 10 months to 8 years. Collars weighing 1.1 to 1.2 kg appeared to cause no adverse effects on wolves. Transmitters provided an average of 29 relocations per month when programmed to transmit to the satellite 4-6 hours every 2 days. Average life span of the transmitters was 181 days (range 50-366 days).

We tested relocation accuracy of the new transmitters by allowing them to transmit from nine known locations prior to deployment on wolves. Service Argos, the agency responsible for processing the data and providing relocations, provides users with data concerning the quality of relocations which are referred to as NQs. NQs 1 through

3 reflect relocations from lowest to highest precision. We determined the accuracy of NQs 1 through 3. Error associated with relocations 1 through 3 averaged 728 ±757, 551 ±528, and 336 ±220 m, respectively. Sixty-eight % of the relocations were <734, <556, and <360 m from the known location, respectively. The proportion of high versus low accuracy relocations was related to individual transmitters and whether the transmitter was on an animal. These data indicate that location accuracy is less when transmitters are actually deployed on animals than when they are not deployed on animals. Consequently, location accuracy is probably lower than that reported during this study.

We found significant ($P < 0.05$) directional biases in the relocations provided by satellite transmitters. Relocations were generally biased towards the south and west. We also determined that location accuracy could be significantly improved by exposing at least 1 cm of the satellite antenna outside of the collar.

Our study suggests that future investigators must carefully define study objectives before employing satellite telemetry. Depending upon the level of resolution required, location errors of 200 to 700 m may limit the usefulness of satellite telemetry for assessing localized movements and habitat use. If the habitats of interest are distributed coarsely across the landscape and study animals move

relatively large distances each day, then satellite telemetry may prove to be useful. For species that occupy large areas such as wolves (i.e., 3,653 km^2 territories), detailed movements data may not be required. In these cases, the primary advantages of satellite telemetry are that they provide continuous relocation data regardless of weather and daylight conditions, and relatively low cost per relocation ($44/relocation).

Each wolf satellite transmitter was equipped with a mercury tip-switch and microprocessor which provide data on ambient temperature of the transmitter canister and activity data. Activity data are provided by tip-switches which are triggered by movements of the wolf's neck. We tested two switch orientations in an attempt to determine optimum angle. Switches were placed parallel to the wolf's spine with the anterior end angled at either -4° or 5° relative to the bottom of the canister. We found that the -4° orientation provided higher activity counts than the 5° orientation during both winter and summer. However, the -4° orientation for the tip switch was probably not optimal because activity indices were only correlated with movement for 6 of 22 and 4 of 12 wolves during summer and winter, respectively.

We determined that wolves were more active during summer than winter. We also determined that wolves were

most active in summer between 2200 and 0600 h and winter between 0700 and 1600 h. Summer activity patterns were similar to those reported by Mech (1970) and Ballard et al. 1992).

Ambient air temperatures provided by satellite collars were within the extremes provided by weather stations close to (40 km) the study area. During winter, temperatures provided by the transmitters frequently exceeded the maximums recorded at weather stations and were much more variable. We attributed the relatively high temperatures to behaviors such as curling the body to reduce heat loss, use of relatively warm microenvironments, and use of south-facing slopes. We concluded that satellite telemetry provides useful gross indices of wolf activity but further testing and calibration are necessary to determine optimum angles for orienting mercury tip-switches.

During 1987 through 1991, a total of 85 wolves within 19 packs were radio-collared and relocated (1,123 occasions) from fixed-wing aircraft. Pup sex ratios at capture were significantly biased towards females, yearling sex ratios were equal, and adult sex ratios were biased towards males. We were unable to explain reasons for these differences.

Based upon a literature review, we considered wolf pack territories to be fully defined when >79 relocations were obtained. Average territory size for seven packs was 3,652

km^2, the largest in North America. Larger packs had larger territories than smaller packs, and winter territories (2,474 km^2) were significantly larger than summer (1,251 km^2). Wolf packs maintained year-round territories although four packs moved to caribou winter range. In the latter cases, wolves moved from 64 to 272 km to caribou wintering areas in mid-winter, remained there for several weeks, and returned to their original territory. The same packs did not migrate each year. Caribou wintering grounds appeared to be occupied by both migratory and year-round resident wolves which maintained territories. Our study clarified the popular misconception that wolves in northwest Alaska migrate annually to follow caribou.

Twenty-four % of the radio-collared wolves dispersed from the territories in which they were originally captured. Sex ratios, average age, or distances moved by males and females were not different. Although wolves dispersed during all months of the year, dispersal was most prevalent during April through July.

Wolf densities within a 12,279 km^2 study area were estimated based upon known numbers within radio-marked packs. Spring wolf densities ranged from 2.7 to 4.4/1,000 km^2 in 1987 and 1990, respectively. The wolf population grew at annual finite rates of increase of 1.06 to 1.43 during 1987 through 1989 and then declined at a rate of 0.64

annually. Study area densities were extrapolated to northwest Alaska, and we estimated the wolf population annually ranged from 179 to 786 wolves depending upon season and year.

We found that wolves used different habitats between summer and winter. Flat slopes were used more and moderate slopes used less during summer while moderate slopes were used more than expected during winter. North-facing slopes were used more than expected during summer. Wolves were relocated predominately in spruce (Picea spp.) dominated habitats during both summer and winter. Wolves used alpine herbaceous tundra, mat and cushion tundra, cottonwood, and rock-snow habitats more during summer than winter. Year-round activity of radio-marked wolf packs was classified as follows: traveling or walking, 34%; running, 23%; bedded or resting, 31%; feeding, 8%; and other, 5%. These activity patterns were similar to those found in Minnesota (Mech 1992) except for the high percentage of wolves that we observed wolves running. We attributed this observation to wolves being scared of the aircraft because fixed-wing aircraft have been used for hunting purposes. Wolves were generally found at relatively higher elevations during January through May.

Wolf packs in northwest Alaska regularly began attending wolf den sites by the third week of May. These

dates are somewhat later than wolves in more southerly latitudes (Ballard et al. 1987). Use of den sites appeared to be traditional, as it is in other areas in Alaska (Ballard et al. 1987). Litter sizes averaged 5.3 (SD = 22) and were within the mid-range reported for North America. There were no indications of multiple litters as has been reported in other areas of North America (Harrington et al. 1982, Ballard et al. 1987). These data indicate that productivity in the northwest Alaska wolf population was lower than that in more southerly latitudes.

Annual wolf survival rates averaged 0.59. This rate was probably biased upward since no pups were monitored throughout the year. Generally, wolf survival rates for different sex and age classes were higher during 1987-88 and 1988-89 than during 1989-90 and 1990-91. These differences were attributed to a rabies epizootic within the wolf population during 1989 through 1990 and high harvest rates by humans.

Hunting was the largest cause of wolf mortality (69% of the mortalities); natural causes accounted for 31%. Rabies was the largest (21% of total mortality) cause of natural mortality. Our study was the first to document that rabies could be a significant mortality factor within a wolf population. Red (Vulpes vulpes) and arctic (Alopex lagopus) foxes were the likely vectors to initially infect wolves.

Based upon observed numbers within radio-marked wolf packs, we estimated that this wolf population could sustain close to 50% mortality annually and remain stable.

During the study, we observed wolves on 184 prey carcasses of which 90% were ungulates. Wolves killed 168 and scavenged 16 of the carcasses. Caribou were the most common (51%) prey item followed by moose (42%). Adults of both ungulate species were the most frequently killed age classes, composing 38 and 25% of the kills, respectively. Wolves killed disproportionately more adult and less caribou calves than that found within the caribou population, while moose sex-age classes were killed in the same proportion as in the moose population.

The numbers of caribou which wintered within the wolf study area declined after 1988, and few caribou were within the area during late winter and spring 1989 and 1990. We monitored selected radio-marked wolf packs daily during 1988 through 1990 to determine prey selection and kill rates. From 3 to 6 wolf packs (total of 13 during 3 years) were relocated and backtracked to previous locations an average of 18 days during March and April. These data also showed that caribou and moose were the most frequently killed prey items: 41 and 36% of the prey, respectively. Small packs of 1 to 4 individuals accounted for all observed scavenging activity ($\underline{n}$ = 7 carcasses). Each pack killed on average of

one adult moose equivalent per 6.7 days. Kills were on average heavily consumed (91%), although scavenging by foxes and ravens (Corvus corax) was likely responsible for part of the consumption. We determined that each wolf in the study area had an average of 5.3 kgs of ungulate prey available per day. Kill rates were correlated with pack size ($P = 0.03$), but kgs available per wolf per day were not ($P = 0.67$). We combined our study results with those from several other areas of North America where caribou and moose were the principal prey and found that both of the above variables were significantly correlated ($P < 0.05$) with pack size. We concluded that pack size was a significant determinant of kill rates and food availability, but that these types of data contain considerable variation and must be carefully evaluated.

During the kill rates study, we documented that, when caribou left the study area during late winter and spring, wolves switched from preying primarily on caribou to preying on moose. Moose have recently colonized (1940s and 1950s) northwest Alaska and now exist at relatively low densities (e.g., 166/1,000 km^2) throughout the area. Historical reports suggested that wolves followed migratory caribou to winter and summer ranges. Our study indicated that, although some wolves occasionally migrate with caribou, most wolf packs maintain year-round resident territories. We

suspected that the establishment of low density moose populations has provided an alternate prey base so that wolves no longer have to follow migratory caribou to sustain themselves. Based upon marrow fat values, it appeared that wolves were killing relatively healthy adult caribou but adult moose that were in marginal condition. The latter characteristic may indicate that either winter conditions were worse within the moose area from which caribou migrated or perhaps that moose habitat in northwest Alaska may be less than optimal; the area is on the fringe of the species distribution.

Based upon our study, we extrapolated observed wolf densities and kill rates to estimate the numbers of caribou and moose killed annually in northwest Alaska. We estimated that wolves were annually killing about 28,000 (6-7%) of 417,000 caribou. When caribou migrate and wolves switch to preying primarily on moose, we estimated that wolves were killing from 11 to 14% of the moose population annually. Based upon available prey biomass, we also estimated that northwest Alaska could support about 16 wolves/1,000 km^2; a density far higher than that observed during this study (i.e., 2.6-6.6/1,000 km^2). We suggested that the large caribou population may allow wolves to reach relatively high densities if they migrated and human harvests were reduced. However, if wolves did not migrate, predation on local moose

populations could result in at least a lower moose population and possibly extinction of some populations. Although many conservationists would argue that northwest Alaska could support a much larger wolf population based upon caribou biomass, management and maintenance of moose populations would be difficult given the prey selection and kill rates observed during this study.

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