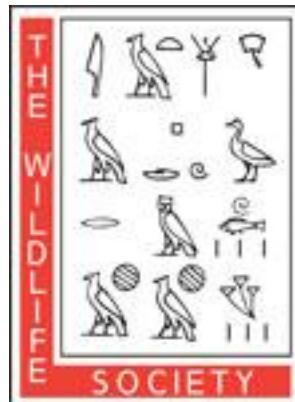


WILEY



Ecology of Wolves in Relation to a Migratory Caribou Herd in Northwest Alaska

Author(s): Warren B. Ballard, Lee Anne Ayres, Paul R. Krausman, Daniel J. Reed and Steven G. Fancy

Source: *Wildlife Monographs*, Apr., 1997, No. 135, Ecology of Wolves in Relation to a Migratory Caribou Herd in Northwest Alaska (Apr., 1997), pp. 3-47

Published by: Wiley on behalf of the Wildlife Society

Stable URL: <https://www.jstor.org/stable/3830776>

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/3830776?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>

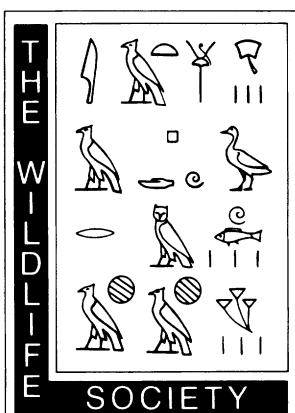


Wiley and Wildlife Society are collaborating with JSTOR to digitize, preserve and extend access to *Wildlife Monographs*

WILDLIFE MONOGRAPHS

(ISSN:0084-0173)

A Publication of The Wildlife Society



ECOLOGY OF WOLVES IN RELATION TO A MIGRATORY CARIBOU HERD IN NORTHWEST ALASKA

by

WARREN B. BALLARD, LEE ANNE AYRES, PAUL R. KRAUSMAN,
DANIEL J. REED, AND STEVEN G. FANCY

NO. 135

APRIL 1997



FRONTISPICE. The Purcell Mountain Pack leaves the lowlands and heads for upland areas where caribou are more available and snow depths are more shallow (photo by W. Ballard).

ECOLOGY OF WOLVES IN RELATION TO A MIGRATORY CARIBOU HERD IN NORTHWEST ALASKA

WARREN B. BALLARD

Alaska Department of Fish and Game, P.O. Box 1148, Nome, AK 99762¹

LEE ANNE AYRES

U.S. National Park Service, P.O. Box 1029, Kotzebue, AK 99752²

PAUL R. KRAUSMAN

School of Renewable Natural Resources, 325 Biological Sciences East Building, University of Arizona, Tucson, AZ 85721

DANIEL J. REED

Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701

STEVEN G. FANCY

U.S. Fish and Wildlife Service, P.O. Box 44, Hawaii National Park, HI 96718

Abstract: There is a paucity of data concerning wolf (*Canis lupus*) demography, movement patterns, and predation characteristics in relation to migratory caribou (*Rangifer tarandus granti*). Consequently, during 1987 through 1992, we studied wolves and the Western Arctic Caribou Herd in northwestern Alaska. We captured and radio collared 86 wolves in 19 packs and relocated them on 1,830 occasions. Wolf packs usually did not follow migratory caribou but maintained year-round resident territories that averaged 1,868 km². However, during years when caribou were absent and moose (*Alces alces*) densities were low, up to 17% of the radio-marked wolf packs followed migratory caribou and then returned to their original territory for denning.

Radio-collared wolves ($n = 21$) dispersed primarily during April through September. Spring wolf densities increased from 2.7 to 4.4 wolves/1,000 km² during 1987 through 1990, and then declined to 1.5 wolves/1,000 km² following a rabies epizootic.

Annual wolf survival rates averaged 0.552 (range = 0.464–0.656). Annual survival during 1990–91 and 1991–92 was lower than other years due to a rabies epizootic. Overall, hunting was the main cause of death (69%) for wolves ($n = 52$). Most (63%) mortality occurred during December through March when snow cover permitted wolf hunting from snowmobiles.

Caribou and moose composed 51 and 42%, respectively, of the kills observed during the study; 59% of caribou and 64% of moose kills were adults. Ungulate kills averaged 4.6/wolf/100 days and provided 5.3 kg of available food/wolf/day. In northwest Alaska, caribou were the principal prey when present within areas used by wolves. However, when caribou densities were <200/1,000 km², wolves switched to preying on resident moose.

Wolves within the range of the Western Arctic Caribou Herd killed 6–7% of this caribou population annually. Caribou left wolf pack territories during winter, and wolves switched to preying on moose for approximately 4 months of each year. Wolves killed from 11 to 14% of the moose population annually. Wolf densities were limited by hunting and trapping, and wolf predation at levels found in 1987–91 did not strongly limit caribou population growth. However, existing wolf populations may be able to regulate local, low-density moose populations that have become established during the past 40 years.

WILDL. MONogr. 135, 1–47

Key words: Alaska, caribou, demography, migration, moose, predation, wolves.

¹ Present address: Arizona Game and Fish Department, 2221 West Greenway Road, Phoenix, AZ 85023.

² Present address: Alaska Department of Fish and Game, P.O. Box 689, Kotzebue, AK 99752.

CONTENTS

INTRODUCTION	6	Mortality	22
Acknowledgments	7	Hunting and Trapping	22
STUDY AREA	7	Allowable Mortality Rates	24
METHODS	10	Feeding Ecology	24
Territory Sizes, Movements, and Dispersal	10	Distribution and Abundance of Caribou	27
Survival, Mortality, and Physical Condition	11	Kill Rates	27
Wolf Density	12	Age and Physical Condition of Ungulate Prey	35
Kill Rates	12	EFFECTS OF WOLF PREDATION ON	
Statistical Tests	12	WESTERN ARCTIC CARIBOU HERD	
RESULTS AND DISCUSSION	13	AND MOOSE	35
Capture and Telemetry Results	13	Effects on Caribou	35
Territory Sizes and Movements	13	Effects on Moose	37
Dispersal	18	CONCLUSIONS	39
Wolf Density	19	LITERATURE CITED	41
Survival	21	APPENDIX	45

INTRODUCTION

The Western Arctic Caribou (*Rangifer tarandus granti*) Herd (WACH) has historically been one of the largest caribou herds in North America and is the largest in Alaska (Davis et al. 1980, Davis and Valkenburg 1985). It is an important resource for human subsistence and recreational uses. The herd was thought to number between 200,000 and 300,000 individuals during the 1950's and 1960's, but declined in the 1970's to a low of about 75,000 in 1976. Several factors caused the decline (Davis et al. 1980), but excessive human harvests and wolf (*Canis lupus*) 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). Assuming that the 1976 estimate of 75,000 caribou was accurate (Davis et al. 1980), the WACH increased at an annual finite rate of increase of 1.12 ($r = 0.11$) to 417,000 by 1991 (Fig. 1). In 1984 the Alaska Board of Game approved a WACH management plan that stated that the highest management priority was to prevent the herd from declining to low numbers (Alas. Dep. Fish and Game 1984). To avoid future catastrophic declines, it was deemed impera-

tive that caribou harvests, wolf predation, 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 1940's and early 1950's, the Federal government used poison and aerial shooting to reduce wolf populations (Kelly 1954). Several estimates of wolf numbers within the range of the WACH have been made since the early 1950's, but their accuracy is unknown. R. O. Stephenson (Alas. Dep. Fish and Game, Fairbanks, unpubl. data) estimated wolf density at 6/1,000 km² ($N = 720$ wolves) in 1977, whereas Quimby (1982) estimated the density at 6/1,000 km² for 85% of the area and 1.9–2.6 wolves/1,000 km² for 15% of the area ($N = 476$ wolves) in 1981. Wolf densities within our study area were estimated at 12.9/1,000 km² in spring 1977 (Davis and Valkenburg 1981). James (1983) thought that because of reduced harvests, 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 1980's, the apparent lack of wolf population response and reported low numbers of wolves observed by members of the public (James 1984, Larsen and James 1987) created interest in determining the exact status of

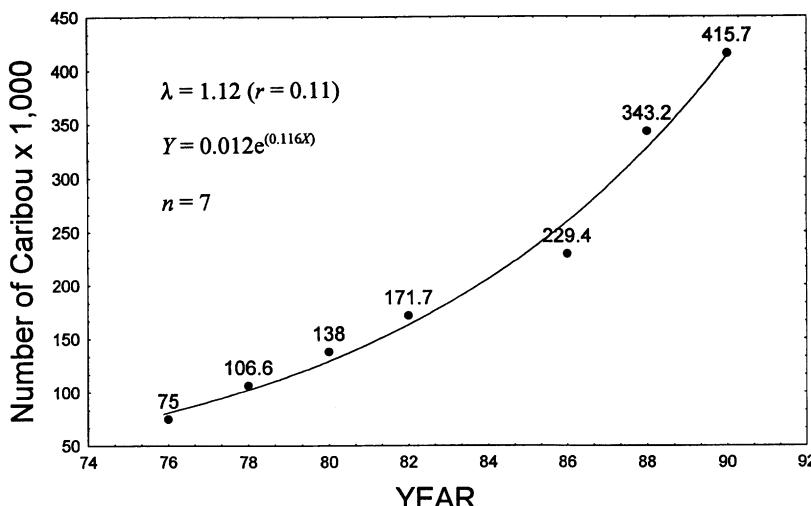


Fig. 1. Projected population growth of the Western Arctic Caribou Herd based upon population estimates obtained during 1976 through 1992. Population estimates were originally presented by Davis and Valkenburg (1978), Machida (1992), and J. R. Dau (Alas. Dep. Fish and Game, Kotzebue, unpubl. data).

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 demography, movement patterns, and diet of wolves in relation to migratory movements of caribou in northwest Alaska and thus quantify the effects of wolf predation on the WACH.

Acknowledgments.—Many individuals participated in various aspects of this study. First, K. R. Roney was instrumental in initiating the study and participated in many aspects of the field work. L. G. Adams, J. W. Coady, A. L. Lovaas, and J. A. Stroble supported this study and helped to insure it was adequately funded. Salary for the senior author during data analysis and manuscript preparation was provided by LGL Alaska Research Associates, Inc., and U.S. National Park Service. T. H. Spraker, C. R. Rodgers, and J. D. Rood were largely responsible for finding wolves for radio collaring. E. D. Penttila, Evergreen Helicopters; B. L. Lofstedt, Kenai Air Alaska; and K. G. Butters and M. J. Wilton, Transalaska Helicopters, Inc., safely and efficiently piloted helicopters during tagging operations. R. A. Brudebaker, R.

Bunn, J. W. Coady, J. R. Dau, D. D. James, R. R. Kemp, D. N. Larsen, S. Machida, K. Mawhinney, R. R. Nelson, J. R. Peterson, K. R. Roney, T. E. Smith, M. A. Spindler, A. M. Wildman, D. E. Witmer, and C. L. Yoder participated in various aspects of the study. R. E. Forrest and K. M. Klug volunteered during summer 1989 and summer 1990, respectively. E. K. Brooks and F. M. Forrester typed tables and several drafts of the manuscript. P. J. Kircher prepared many of the figures. M. A. Cronin and staff of LGL Alaska Research Associates, Inc., deserve a special thanks for their support during data analysis and preparation of this text. A. F. Cunning, E. H. Follman, G. J. Forbes, J. A. Kershaw, R. W. Mannan, O. E. Maughan, W. W. Shaw, V. Van Ballenberghe, H. A. Whitlaw, and M. J. Zwolinski reviewed earlier drafts of the manuscript. The final manuscript was greatly improved as a result of constructive criticism provided by T. K. Fuller, R. L. Kirkpatrick, T. J. Kirkpatrick, and F. Messier.

STUDY AREA

Davis et al. (1980) defined the range of the WACH as encompassing 362,600 km²

in northwest Alaska. During spring 1987, we selected a wolf study area (Fig. 2) that appeared representative of caribou winter range (James 1983). The wolf study area was 12,280 km² and was contained largely within Game Management Unit (GMU) 23 (approx 119,140 km²). We refer to GMU 23 as northwest Alaska.

During summer 1988, a wildfire burned across 845 km² within and north of the study area. After the 1988 fire, most caribou wintered south of the burn in the Selawik and Nulato hills (Spindler 1989, Machida 1992) and consequently south of the wolf study area. Because of annual variation in the use of the refuge as a wintering area prior to the fire, it cannot be assumed that the fire caused the caribou to winter elsewhere. However, for the short term the fire may have been a significant factor.

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 southward and by late October and November about half of the herd was south of the wolf study area (Machida 1992). Therefore, caribou used the wolf study area primarily during autumn and spring migrations. During these times, an estimated 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).

Topography is varied with broad, relatively flat plains along the major river systems grading into rolling hills and rugged steep mountainous terrain in major mountain ranges, such as the Purcell and Baird mountains. Elevations within the study area range from near sea level along the Kobuk and Selawik rivers to 1,168–1,231 m for several mountain peaks that rise abruptly from valley floors.

Vegetative cover of the area is diverse and includes unvegetated sand dunes

(largest being the Greater and Little Kobuk sand dunes; approx 8–75 km²), gravel bars, rock screes, lakes and ponds of various sizes, wetlands, and marshes; these grade 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 includes sparse-to-dense taiga scrub forests of white and black spruce (*Picea mariana*) that grade into, or contain, alpine and arctic tundra. Small tundra lakes and wetlands are prominent along the Selawik River. The area is bisected by the Kobuk, Selawik, and Huslia river systems.

The area has a maritime climate during ice-free periods and has long cold periods during winter months (U.S. Dep. Inter. 1987). Temperature extremes ranged from 32 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 in water equivalents averaged 6–8 cm in lowlands and ≤12 cm in upland areas. Half of the precipitation occurred during July and August. Winter winds often resulted in hard-packed snow and large drifted areas. Because of severe winter winds, snow depths ranged from almost nil in upland windblown areas to several meters in low riparian areas.

Mammals common to the study area include brown (*Ursus arctos*) and black bear (*U. 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 (*Alces alces*), Dall sheep (*Ovis dalli*), muskox (*Ovibos moschatus*), snowshoe hare (*Lepus americanus*), and several species of squirrels (Sciuridae) and microtine (Microtinae) rodents.

Moose colonized northwest Alaska during the 1940's and early 1950's (J. R. Dau

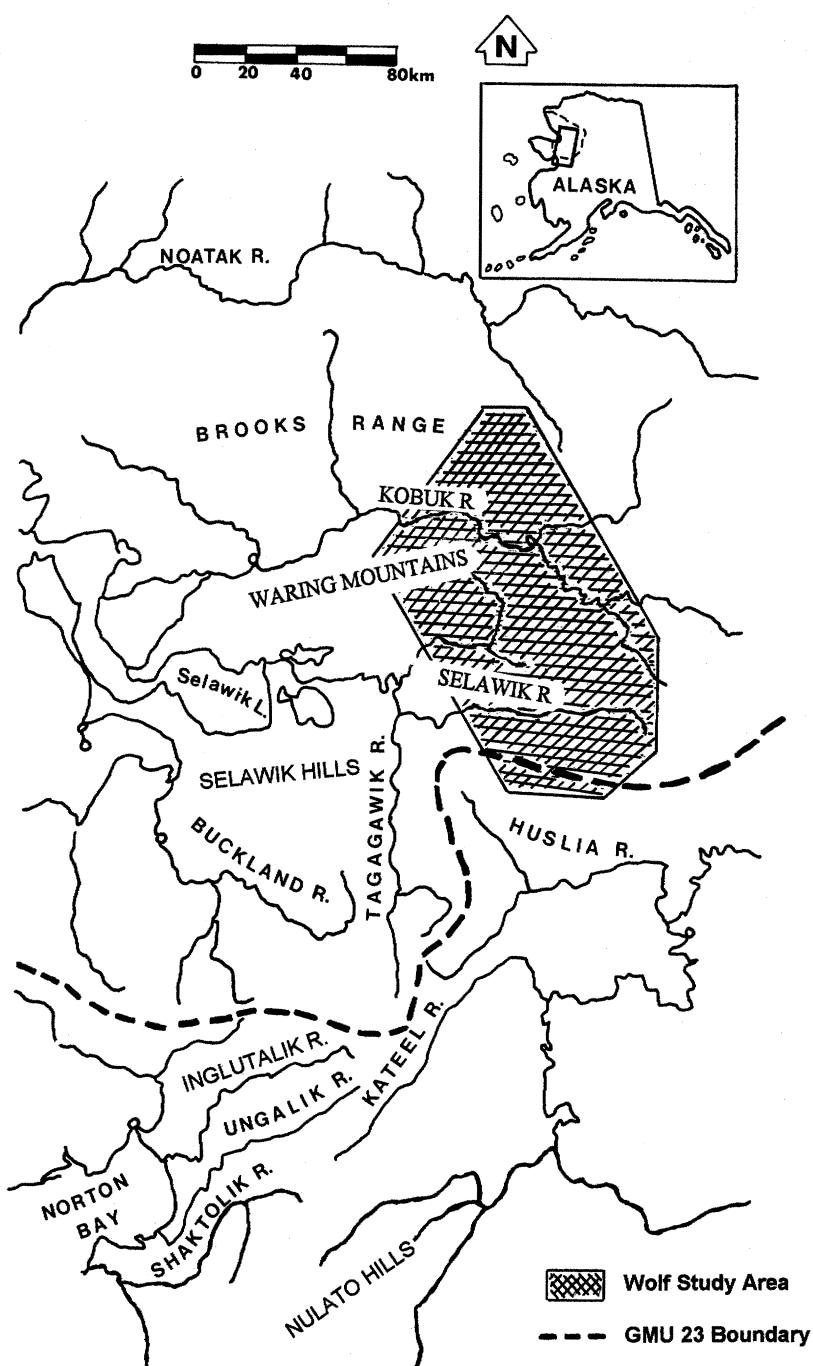


Fig. 2. Boundaries of wolf study area in northwest Alaska, April 1987 through July 1992.

and L. A. Ayres, Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 24pp., 1993). Moose populations increased in all areas of northwest Alaska through the mid-to-late 1980's. Dau and Ayres (1993 unpubl. rep. cited above) suggested that moose populations in some portions of northwest Alaska began declining about 1990. Reasons for the apparent decline were not known, but severe winters and excessive predation by wolves and brown bears were proposed (Dau and Ayres, 1993 unpubl. rep. cited above). Whether the moose population was exhibiting the classic eruption, decline, and stabilization phase suggested by Caughley (1970) was unknown. Dau and Ayres (1993 unpubl. rep. cited above) 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 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 the 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 study area were estimated at 166/1,000 km² in October 1985 (Larsen et al. 1986). Even though the 90% confidence interval for

that estimate was large ($\pm 102\%$), the estimate (1,864) was similar to an estimate ($1,799 \pm 25\%$) obtained during a December 1984 survey (Larsen et al. 1986).

METHODS

We used acceptable field methods (Am. Soc. Mammal. 1987) while conducting our research. We located wolves for capture, usually during March or April, after fresh snowfall of ≥ 8 cm. Experienced pilot–observer teams in fixed-wing aircraft (Piper PA-18) searched lake shores, ridge lines, 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 (Ballard et al. 1982, 1991). Each immobilized wolf was sexed, aged, 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.). Tooth eruption and wear patterns were used to differentiate among pups (assumed 1 Jun birth date), yearlings, and adults.

We attempted to locate instrumented wolf packs within the study area approximately once every 2 weeks throughout the year. We recorded the date, time, number, sex and age of associates, activity, and type of habitat for each wolf location on standardized forms.

Territory Sizes, Movements, and Dispersal

We estimated annual and seasonal territory sizes from all pack relocations (excluding obvious extraterritorial forays, dispersals, and migratory movements) using the minimum convex polygon method (Mohr 1947) and the McPAAL software package (M. Stuwe and C. E. Blohowiak, Conserv. Res. Cent., Natl. Zool. Park, Smithsonian Inst., Front Royal, Va., 1985). We defined winter as the period from 1 October through 30 April and summer from 1 May through 30 September.

Several investigators have examined the

number of relocations necessary to adequately describe wolf territory size. Fritts and Mech (1981) determined that in northwest Minnesota an average of 79 relocations was necessary when packs were located over a period of ≤ 1.5 years. Messier (1985) suggested that year-long territories were defined after 40–80 daily relocations, whereas Carbyn (1983) and Fuller and Snow (1988) determined that about 30–35 relocations were necessary to describe 85–90% of winter territory size. Ballard et al. (1987) estimated that approximately 60 relocations were required to adequately define total territory sizes over a period of 8 years in south-central Alaska where territory sizes were commonly $> 1,500 \text{ km}^2$. Based on these discussions, we calculated territory sizes only for those packs with > 30 relocations.

We classified wolf movement behavior into 4 categories: (1) resident—wolves remained within annual territory boundaries, (2) extraterritorial forays—usually single wolves that temporarily left their territories for varying time periods and distances but returned to the original territory, (3) dispersal—single wolves that permanently left their original territory and did not return (some of which may have been on extraterritorial forays but died), and (4) migratory—entire packs that left observed territory boundaries during winter in the same direction as migratory caribou and then returned to the original territory for denning. We classified a wolf as missing when we could no longer locate it, and its fate was unknown. Seasonal shifts in territory use occurred when wolf packs made movements away from previously used areas within their territory but remained within the territory boundaries.

Because our frequency of relocations was not sufficient to determine exact dates of dispersal, we used median dates. The median date for each dispersal event was determined from the date of the last known occurrence within the original territory to when the dispersing wolf was known to be absent from that territory. Annual dispersal rates were calculated using methods described by Heisey and Ful-

ler (1985). For these analyses, dispersal was considered another source of “disappearance.”

Survival, Mortality, and Physical Condition

Annual wolf survival rates for each sex and age class were estimated by extrapolation of daily survival rates using methods described by Heisey and Fuller (1985) and Fuller (1989). Examination of rates and sources of mortality in this study suggested that the biological year should be divided into 2 intervals: winter = December–April; summer = May–November. Wolves were added to the analysis on the date they were captured and radio collared. When radio contact was lost and fate was unknown, they were censored from the data set on the date of last observation. When dates of last observation and known death spanned several months, the median date was used.

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 1989–90 season. Since the 1988–89 season, the hunting 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 to exit the plane before firing. The latter procedure is referred to by Alaska trapping regulations as “land and shoot trapping.” The procedure could be repeated as long as the aircraft did not harass the wolves. Beginning in 1988–89, lands administered by the U.S. National Park Service were closed to the “land and shoot trapping method.” This included Kobuk Valley National Park within the study area. Beginning in 1991–92, this ban was extended to all areas in northwest Alaska. Regulations require all hunters and trappers to present hides of harvested wolves to state officials for recording and sealing. Data such as sex, color, and method and date of take are recorded on stan-

dard forms, and a seal is placed on each hide.

We determined the cause of death of ungulate carcasses observed while locating instrumented wolf packs using criteria described by Stephenson and Johnson (1972, 1973), Peterson (1977), Peterson et al. (1984), Ballard et al. (1987), and Fuller (1989). These causes included wolf killed, bear killed, hunter killed, scavenged, winter killed (starvation), or unknown. We differentiated fresh predator-killed carcasses from those that were scavenged by the presence of fresh blood, both predator and prey prints, and whether the carcass was covered with hard-packed snow. From fixed-wing aircraft, we determined sex and relative age (calf or adult) of wolf-killed ungulate carcasses by presence and/or shape of antlers, presence of vulva patch, body size, and pelage (Peterson 1955, Skoog 1968, Ballard et al. 1987). We estimated age of 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 (13.5% of 166 carcasses), we examined ungulate carcasses *in situ* to confirm cause of death and 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). We regressed the marrow fat content in mandibles and other bones to the femur standard (Ballard et al. 1981a, Davis et al. 1987).

Wolf Density

Spring and autumn wolf densities within the study area were estimated based on known numbers of wolves within radio-marked packs and their respective territory sizes. These estimates were extrapolated to other portions of GMU 23 and other areas within the range of the WACH. 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 addi-

tional areas, we conducted 3 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 1988).

Kill Rates

During late winter and early spring 1988 through 1990, we intensively monitored 3–6 wolf packs on a daily basis to determine kill rates. We defined kill rate as the number of ungulates killed per wolf per day. 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 (co-author) and D. N. Larsen (Alas. Dep. Fish and Game, Ketchikan) 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. The relative availability of caribou as prey during March and April of each year was evaluated and rated based upon the proportion of radio-collared caribou (randomly captured when they crossed the Kobuk River during late Aug-Oct) from the WACH (Machida 1992) located within the wolf study area and by our observations of the numbers of caribou within the area during daily flights.

Statistical Tests

Comparisons of medians were conducted with Mann-Whitney *U* tests and Krus-

kal-Wallis ANOVA (Ott 1988). Frequency data were compared by Chi-square tests. Average wolf weights were compared with Tukey's test (Sokal and Rohlf 1969:238). Rate of increase for the WACH was calculated by log_e transformations of herd estimates fit by least squares regression (Caughley 1978, Neter et al. 1989). Correlations between pack sizes and territory sizes, time at kills, kill rates, and prey weight consumed per wolf per day were analyzed with Spearman's rank correlation r_s (Conover 1971). For illustrative purposes, we used linear, logistic, or exponential regression models to depict relationships for significant Spearman rank correlations. We compared individual sex-age survival rates by Z test (Heisey and Fuller 1985). We evaluated the effects of age, sex, and year on survival using hierarchical log-linear models (Zar 1984). Analysis of covariance (ANCOVA) procedures (SYSTAT; Wilkinson et al. 1992) were used to compare intercepts and slopes for exponential rates of increase based on percent overwinter mortality between large and small packs. Unless stated otherwise, $P \leq 0.05$ was necessary for significance. In general, because of relatively small sample sizes, the power to detect significant differences was low, and many nonsignificant differences could have been due to low power. Parameter estimates are presented as point estimates ± 1 standard error.

RESULTS AND DISCUSSION

Capture and Telemetry Results

We captured and radio collared 86 wolves 102 times in northwest Alaska during April 1987 through April 1991 (Appendix). No wolves were killed as a result of immobilization, but 1 wolf was killed for rabies testing after it bit one of the tagging personnel.

Sex and age composition of radio-collared wolves was 12 male versus 22 female pups ($X^2 = 1.50$, $P = 0.22$, tested against an expected 50:50 sex ratio), 7 male versus 7 female yearlings, and 25 male versus 13 female adults ($X^2 = 1.94$, $P = 0.16$).

Table 1. Average spring weights (kg) of wolves captured in northwest Alaska during April 1987 through 1991.

Age	Sex ^a	n	\bar{x}	SE
Adult	M	23	47.3	0.8
Adult	F	17	42.2	1.0
Yearling	M	8	46.2	1.0
Yearling	F	9	41.9	1.2
Pup	M	10	44.6	1.3
Pup	F	16	37.5	1.0

^a Because some wolves were captured ≥ 1 time at different ages, data do not represent initial sex ratios at capture.

Adult males had a mean weight of 47.3 kg and were the heaviest sex-age class examined (Table 1). We were unable to detect significant differences ($P > 0.05$) between weights of pup or yearling males and those of adult males, indicating that male wolves attained most of their weight by 11 months of age. Female pups were significantly ($P < 0.05$) lighter than all other sex-age classes (Table 1). 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, 86 radio-collared wolves within 19 wolf packs were relocated from fixed-wing aircraft on 1,830 occasions. Total relocations ($n = 1,123$) for each of 19 packs averaged 62 ± 14 (range = 6–209), and length of radio contact averaged 736 ± 120 days (Fig. 3). Each pack was relocated at an average interval of 22.4 ± 3.2 days.

Annual territory size for packs located on ≥ 30 occasions averaged $1,868 \pm 249$ km² (Table 2). There were no differences in annual average territory sizes among years ($H = 0.57$, $P = 0.90$). Annual territory sizes were correlated with both pack size ($r_s = 0.56$, $P = 0.04$) and numbers of relocations ($r_s = 0.53$, $P = 0.05$). Pack size and numbers of relocations were not correlated ($r_s = 0.06$, $P = 0.85$). Stepwise multiple regression of pack size and number of relocations on annual territory size suggested that pack size accounted for most of the variation in territory size (pack

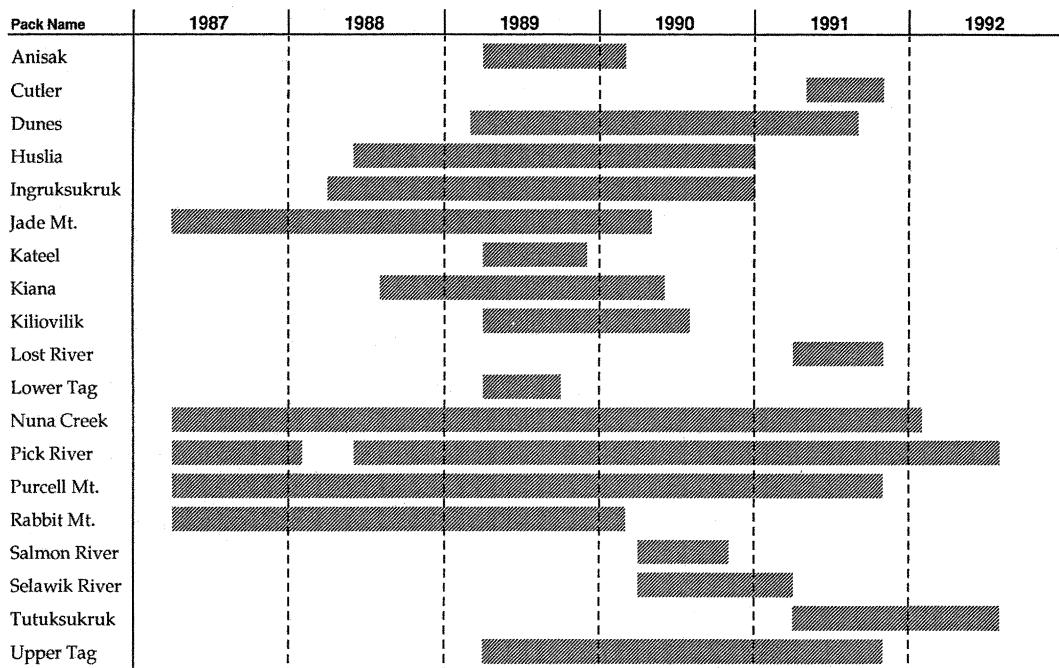


Fig. 3. History of radio contact with individual wolf packs studied in northwest Alaska, April 1987 through July 1992. Horizontal bars indicate periods of continuous radio contact.

size, partial $r^2 = 0.44$, $P = 0.01$; no. relocations, partial $r^2 = 0.19$, $P = 0.003$).

Annual winter territories averaged $1,372 \pm 175 \text{ km}^2$ and there were no differences among years ($H = 1.07$, $P = 0.78$). Numbers of relocations obtained during winter were not correlated with territory size during winter ($r_s = 0.32$, $P = 0.26$), but winter pack size was correlated with territory size ($r_s = 0.55$, $P = 0.04$).

Assuming >30 relocations also were necessary to define territory sizes during summer, no summer territories were adequately defined (Table 2). However, there was no correlation between numbers of summer relocations ($r_s = 0.43$, $P = 0.12$) or pack size ($r_s = 0.29$, $P = 0.32$) with territory size during summer. Visual inspection of winter territories suggested they were consistently larger than summer territories. However, summer territories may have been inadequately defined due to low numbers of relocations. We, therefore, randomly sampled winter data sets so that the numbers of summer and winter relocations were equal (termed adjusted

winter territory size). Both adjusted ($\bar{x} = 1,076 \text{ km}^2$, $U = 51.0$, $P = 0.03$) and unadjusted ($\bar{x} = 1,372 \text{ km}^2$, $U = 31.0$, $P = 0.002$) winter territory sizes were larger than territories used during summer.

Fuller (1989) and Hayes et al. (1991) reported no differences in summer versus winter territory sizes in Minnesota and Yukon Territory, respectively. Although our estimates of summer territory size may have been biased due to an inadequate numbers of relocations, we suggest that winter territories in our study were larger than those during summer due to large differences in density and distribution of prey between seasons. Relatively low prey densities during winter caused wolves to range over large areas to find vulnerable prey. Perhaps more importantly, both caribou and moose were available during summer within each pack territory. The presence of a den also may have limited the distances that wolves could effectively hunt and still feed pups during summer.

Some wolves were apparently forced to migrate after caribou left their pack area

Table 2. Seasonal and annual territory sizes for radio-marked wolf packs in northwest Alaska, 1987–91.

Year ^a	Pack name	Summer ^b			Winter			Annual	
		km ²	No. of locations	Pack size	km ²	No. of locations	Pack size	km ²	No. of locations
1987–88	Jade Mt.	322	11	2	762	36	2	938	47
	Nuna Creek	884	13	9	987	39	8	2,368	52
	Purcell Mt.	236	17	9	1,833	41	12	1,848	58
	Rabbit Mt.	468	13	5	1,243	38	5	1,581	51
	\bar{x}	478	13.5	6.3	1,206	38.5	6.8	1,684	52.0
	SE	144	1.3	1.7	231	1.0	2.1	297	2.3
									6.8
1988–89	Ingruksukruk	900	29	12	1,252	30	12	1,821	43
	Nuna Creek	2,190	24	11	1,745	40	14	4,312	64
	Purcell Mt.	483	11	16	626	33	15	1,046	44
	Rabbit Mt.	296	16	5	2,306	34	6	2,334	50
	\bar{x}	967	20.0	11.0	1,482	34.3	11.8	2,378	50.3
	SE	370	3.5	2.0	310	1.8	1.7	603	4.2
									11.8
1989–90	Dunes	119	11	1	425	26	2	460	37
	Ingruksukruk	900	29	8	1,316	30	6	1,991	59
	Nuna Creek	240	14	18	2,677	41	20	2,719	55
	Purcell Mt.	121	11	13	1,782	25	14	1,898	37
	\bar{x}	345	16.3	10.0	1,550	30.5	10.5	1,767	47.0
	SE	162	3.7	3.1	407	3.2	3.5	409	5.1
									10.5
1990–91	Dunes	393	9	4	514	29	5	745	38
	Purcell Mt.	1,152	13	16	1,746	20	14	2,100	36
	\bar{x}	773	11.0	10.0	1,130	24.5	9.5	1,423	37
	SE	268	1.4	4.2	436	3.2	3.2	479	0.7
Pooled	\bar{x}	621	15.8	9.2	1,372	33	9.6	1,868	47.9
	SE	144	1.7	1.4	175	1.7	1.4	249	2.4
									9.7

^a Biological year: Summer = 1 May–30 September; Winter = 1 October–30 April.^b Summer territories may have been inadequately defined (see Territory Sizes, Movements, and Dispersal).

(see Distribution and Abundance of Caribou). We suspect they moved because moose densities (i.e., <166/1,000 km²) were not high enough to sustain the packs. Overall, a mean of 11% of the radio-marked packs annually migrated with caribou (0 of 5 packs during 1987–88; 2 of 8 packs during 1988–89; 1 of 12 packs during 1989–90; 1 of 8 packs during 1990–91; and 0 of 3 packs during 1991–92). Packs moved 64–272 km (Table 3) to winter range during October through February and returned to their former territories during March through May.

Plots of convex polygons excluding extraterritorial forays, dispersals, and migratory movements suggested that most wolf packs in northwest Alaska were territorial and nonmigratory (Fig. 4). Overlap among wolf territories (Fig. 4) was the result of using convex polygons and changes in use among seasons and years (Ballard et al. 1987:16). Although some overlap among areas occurred (particularly along territory

edges), packs used the same core areas annually, with outer areas being used in different seasons and years. 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 (pack no. 3, Fig. 4) within the Rabbit Mountain area (pack no. 13) and establishment of the Selawik River Pack (pack no. 15) within the Kiliovilik territory (pack no. 7).

The Anisak Pack, one that migrated during winter 1989–90, occupied an area (pack no. 1, Fig. 4) previously occupied by 2 wolf packs that earlier had been reported as migratory (Stephenson and James 1982). We suspect that many of the packs may be migratory north of the Brooks Mountain Range following caribou to winter range. We reached this tentative conclusion because moose densities north of the Brooks Range are very low (i.e., <100/1,000 km²), presumably allowing very few

Table 3. Summary by sex and age class of wolf dispersals and migratory movements in northwest Alaska, 1987-91.

Type of observation	Pack name	Wolf no.	Sex	Age ^a	Dispersal (km)		Dispersal dates		Median ^a	Status last observation
					Range	Median	Range	Median		
Dispersal	Purcell Mt.	4	F	Adult	16	24 Jun-21 Sep 1988	26 Aug	Paired		
	Pick River	6	M	Adult	328	7 Jul-1 Nov 1987	2 Aug	Alone		
	Nuna Creek	9	M	Adult	375	24 Nov-17 Dec 1987	5 Dec	With existing pack		
	Ingrukskruk	17	F	Yearling	77	22 Feb-4 Apr 1989	2 Mar	Paired		
	Nuna Creek	18	M	Adult	64	31 Mar-1 Jul 1989	1 Apr	Missing		
	Nuna Creek	21	M	Adult	64	3 Jun-17 Aug 1988	7 Jun	Paired		
	Kiana	27	M	Adult	16	1 May 1990	1 May	Missing		
	Dunes	33	F	Adult	106	18 Apr-28 Aug 1990	20 Jul	Missing		
	Nuna Creek	35	F	Yearling	166	2 Apr-7 Apr 1990	5 Apr	Missing		
	Pick River	36	F	Yearling	272	12 Oct 1990-11 Mar 1991	12 Dec	Missing		
	Pick River	38	M	Yearling	148	25 May-6 Sep 1989	21 Jun	Killed		
	Upper Tagagawick	46	F	Yearling	113	6 Nov 1988-27 Mar 1989	21 Jan	Alive		
	Salmon River	57	F	Adult	154	21 Jun-12 Oct 1990	6 Sep	Missing		
	Salmon River	59	M	Adult	64	1 May-14 May 1991	8 May	Alone		
	Pick River	65	M	Yearling	135	1 May 1990	1 May	Alone		
	Pick River	66	M	Adult	77	14 May-28 Aug 1991	2 Jul	Alone		
	Dunes	68	M	Adult	270	20 Jul 1990-11 Mar 1991	31 Aug	Killed		
	Dunes	69	M	Adult	166	5 Dec 1990-3 Mar 1991	18 Jan	Missing		
	Tutuksuk River	80	F	Adult	72	28 Aug-9 Oct 1991	14 Sep	With pups		
	Lost River	83	M	Yearling	142	9 Apr-10 May 1991	24 Apr	Alone		
	Cutler River	87	M	Yearling	154	8 Oct-15 Dec 1991	16 Nov	Killed		
	Ingrukskruk	13	M	Adult	167	22 Feb-4 Mar 1989	Killed	Killed		
	Ingrukskruk	15	M	Adult	167	22 Feb-4 Mar 1989	Killed	Killed		
	Ingrukskruk	17	F	Adult	64	6 Nov-1 Dec 1989	Killed	Killed		
	Ingrukskruk	25	M	Pup	264	14 Nov-10 Mar 1989	Killed	Killed		
	Rabbit Mt.			Adult	85	28 Nov 1989-24 Feb 1990	Killed	Killed		
	Anisak	49	M	Yearling	272	12 Oct-14 Apr 1991	Missing	Missing		
	Pick River	65	M	Adult	272	12 Oct-14 May 1991	Missing	Missing		
	Pick River	66	M							

^a Median date: midrange between last observation when observed withining pack's territory and the date known to be outside the pack's territory.

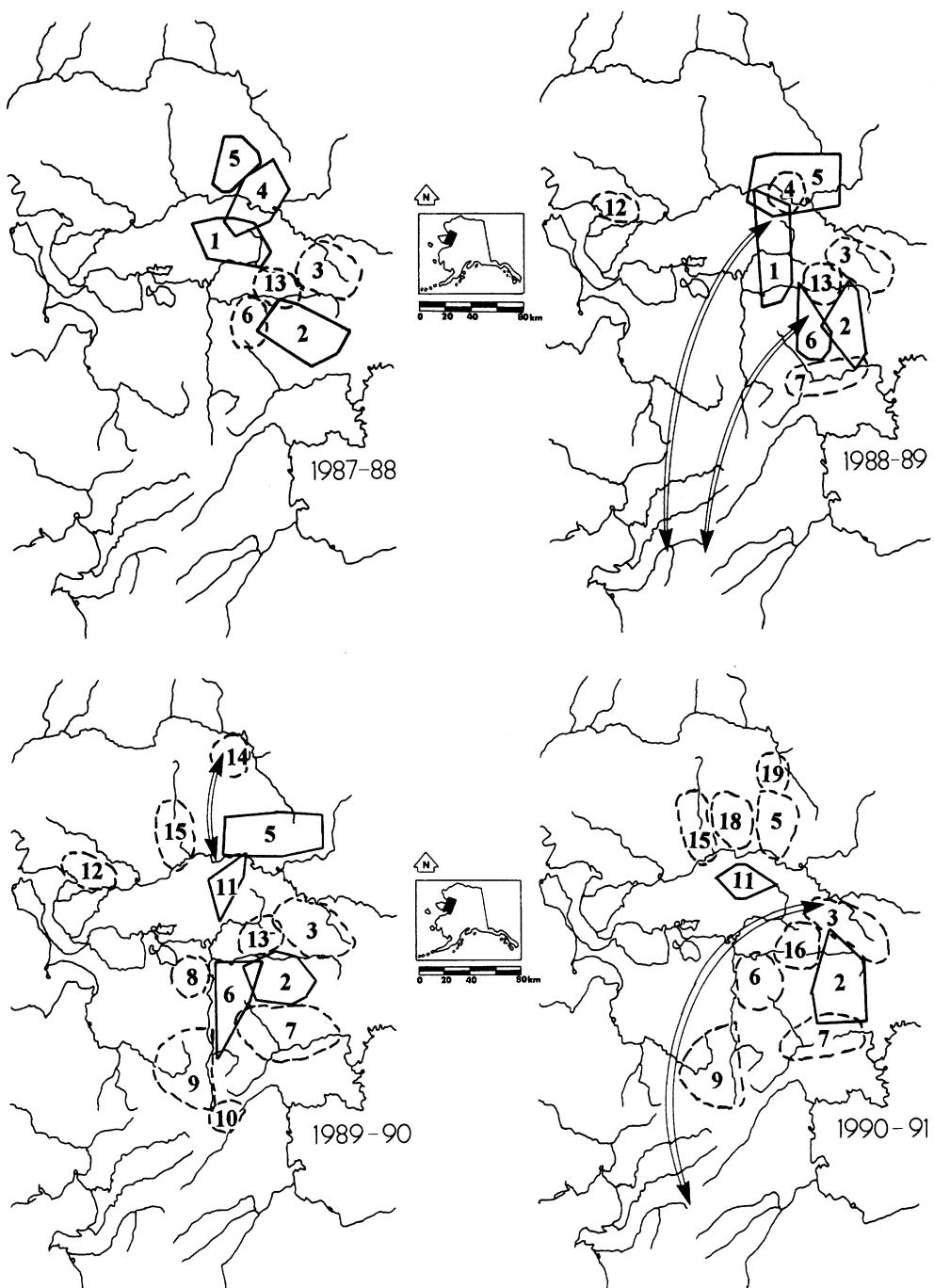


Fig. 4. Annual distribution of 19 wolf packs that were studied in northwest Alaska, April 1987 through July 1992. Heavy solid lines are known territory boundaries based on ≥ 30 relocations/year for radio-marked packs. Dotted lines are suspected pack boundaries based upon combinations of radio-marked animals and track observations. Double arrows indicate migratory movements. Numbers correspond to pack I.D. numbers as in Appendix.

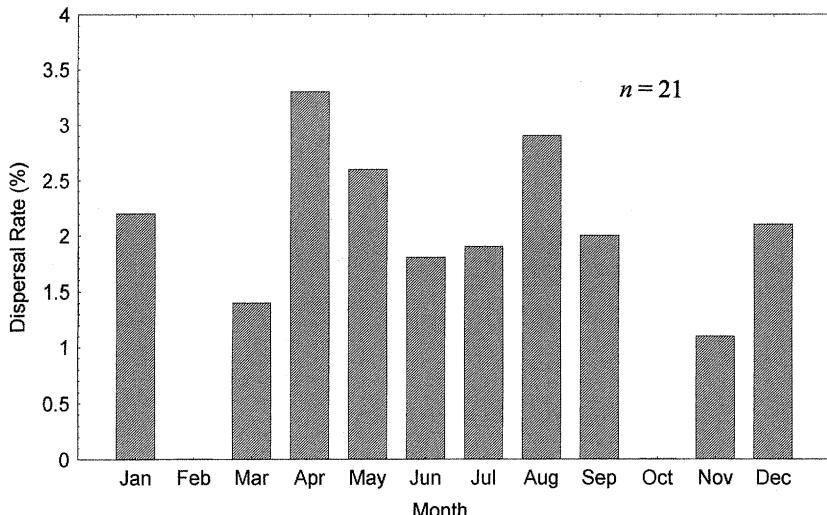


Fig. 5. Average monthly dispersal rates of radio-marked wolves in northwest Alaska, April 1987 through July 1992.

wolves to remain there on a year-round basis when caribou leave the area. However, 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, Kotzebue, pers. commun.). In this area, 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 south (up to 225 km) of the wolf study area. Tracks of ≥ 5 wolf packs totaling 19–28 wolves were observed. 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 the spatial relationships among these groups are unknown.

Dispersal

During our study, 21 wolves (13 M, 8 F) (25% of total) dispersed from the territories in which they were originally radio

collared (Table 3). We found no differences in annual dispersal rates between yearlings and adults (0.153 vs. 0.170). Annual dispersal rates of radio-marked wolves averaged 0.16 (range = 0.11–0.21). Although we could not detect any differences in annual dispersal rates among years, highest rates occurred during the rabies epizootic (0.21 and 0.19 for 1990–91 and 1991–92, respectively).

We were not able to detect differences in the sex ratio of dispersing versus non-dispersing wolves ($X^2 = 1.32$, 1 df, $P = 0.25$). On average, males dispersed 154 ± 30.2 km, whereas females dispersed an average distance of 123 ± 29.4 km; we were unable to detect significant differences between sexes ($U = 43.0$, $P = 0.84$) in distances moved. Average age of dispersing males was 3.4 ± 0.8 years, whereas females averaged 2.9 ± 0.4 years; 31% of male and 43% of female dispersers were 12–24 months of age at time of dispersal. Only 1 radio-collared pup (≤ 12 months of age) dispersed during the study.

Wolves dispersed from their original territories during all months of the year except for February and October. Dispersal in northwest Alaska was most prevalent during April through September (Fig. 5).

Status of dispersing wolves at the time of last observation was variable (Table 3).

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 in August accompanied by 5 pups and was last observed 72 km from its original territory within the area previously or currently occupied by another pack (Dunes Pack). No dispersing wolves were known to have died from rabies (*see Mortality*). Thirteen single wolves were observed making extraterritorial forays.

Ballard et al. (1987) reported that 28% of radio-collared wolves in south-central Alaska dispersed over an 8 year period; 40–50% were yearlings, and more males than females dispersed. Fuller (1989) reported that 35% of radio-collared wolves dispersed over a 7-year period in Minnesota, and there were no differences in dispersal rates by sex. Annual age-specific dispersal rates in that study were as follows: 10% for pups, 49% for yearlings, and 17% for adults (Fuller 1989:18). Annual dispersal rate of yearling and adult wolves on the Kenai Peninsula, Alaska, averaged about 19% (Fuller 1989). Hayes et al. (1991) reported dispersal rates (29% over a 7-yr period) 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 likely determined by such factors as wolf and prey densities, pack sizes, territory sizes, and behavior (Packard and Mech 1980, Fuller 1989). Peterson et al. (1984) suggested that a higher level of social stress in relatively large packs prompted more frequent extraterritorial move-

ments. This speculation may apply to dispersal rates in many wolf populations. Wolves appear to disperse from original territories during all months of the year, except in arctic and subarctic areas where peak dispersal occurs during late spring through summer (Peterson et al. 1984, Ballard et al. 1987, Hayes et al. 1991, this study). However, in this study the highest annual dispersal rate occurred following a rabies epizootic when wolf densities were lowest, probably due to destruction of pack social structure following mortalities.

Reported dispersal rates in North America range from 21 to 35% (Fritts and Mech 1981, Peterson et al. 1984, Ballard et al. 1987, Fuller 1989, Hayes et al. 1991). These dispersal rates suggest that wolves are capable of colonizing new habitats if not subjected to high levels of human-caused mortality.

Several 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. 1995). Hayes et al. (1991) suggested that long-distance movements of wolves between Canada and Alaska provided evidence that wolf distribution was dynamic and confirmed the phenotypic relatedness of the northwestem gray wolf (Nowak 1983).

Wolf Density

Spring wolf densities within the study area increased from 2.7/1,000 km² in 1987 to 4.4/1,000 km² in 1990 ($\lambda = 1.11$, Table 4) and then declined to approximately 1.5 wolves/1,000 km² in 1991 ($\lambda = 0.35$) because of a rabies epizootic and heavy human harvests. The autumn wolf population increased at an annual finite rate of increase of 1.22 from 1987 to 1989 and then declined at an annual finite rate of about 0.63 through 1991 (Table 4). The wolf population appeared to begin increasing after 1990 as several packs began to increase in number. One pack in particular, Nuna Creek, increased from 3 to 19 wolves from spring 1991 to autumn 1991, respectively. Explanation for this unusually

Table 4. Number of wolves observed in radio-marked packs during spring and autumn 1987 through 1991 in northwest Alaska and Game Management Unit (GMU) 23. Pack names followed by an asterisk were used for density estimates. Blank space indicates no data whereas 0 indicates no wolves found in area.

Pack name	1987				1988				1989				1990			
	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn
Anisak									2	3						
Cutler River	0	0	0	0	1	1	2	2	5	5	6	6	8	10		
Dunes*									>4	1	7	7	1-2 ^a			
Huslia									9	7	4	4	0	0		
Ingruitsukruk*	4 ^a	10 ^a	10	14	14	9	7	7	1	1	0	0	0	0		
Jade Mt.*	2	2	1	2	1	2	1	2	0	0	0	0	0	0		
Kiana									3	10	1	1				
Kiliavlik*	3 ^a	3 ^a	3 ^a	3 ^a	2	2	2	2	0	0	0	0	0	0		
Lost River													4 ^b	1		
Lower Tagagawick									2	3						
Nina Creek*	8	9	7	15	12	24	16	16	3	3	3	3	19			
Pick River*	4	6	3	8	5	17	8	8	10	10	2	2	4			
Purcell Mt.*	6	12	11	20	10	16	16	16	12	19	9	9	6			
Rabbit Mt.*	3	7	2	8	3	1	1	0	0	0	0	0	0	0		
Salmon River																
Selawik River*																
Upper Tagagawick																
Subtotal (Used for density)	30 (30)	49 (49)	37 (37)	80 (71)	57 (44)	103 (74)	67 (49)	67 (47)	88 (47)	88 (47-48)	55 (29)					
No. lone wolves assumed at 10%	3	5	4	7	4	7	5	5	5	5	5	5	3			
Total Wolves/1,000 km ² c	33	54	41	77	44	81	54	52	52	52	19-20	2	3	32		
GMU 23 population estimate assuming 119,140 km ²	2.7	4.4	3.3	6.3	3.6	6.6	4.4	4.2	4.2	4.2	1.5-1.6	2.6				
Spring finite rate increase	322	524	393	750	429	786	525	500	1.22	1.22	0.64	0.64	310			
Autumn finite rate increase			1.22		1.43		1.05						0.62			

^a Estimates based on track counts, public observations, and harvest records.
^b Could have been remnants of Salmon River Pack.
^c Assuming a study area of 12,279 km².

Table 5. Seasonal^a and annual survival rates^b (sexes and ages pooled) and number of radio-tracking days for radio-collared wolves in northwest Alaska during 1987–88 through 1991–92.

Year	No. of radio-tracking days	Summer		Winter		Annual	
		Rate	95% CI	Rate	95% CI	Rate	95% CI
1987–88	3,858	0.919	0.778–1.000	0.712	0.484–1.000	0.654	0.430–0.994
1988–89	7,543	0.953	0.867–1.000	0.614	0.454–0.831	0.585	0.427–0.803
1989–90	9,222	0.747	0.610–0.914	0.799	0.655–0.972	0.596	0.449–0.791
1990–91	9,416	0.870	0.758–0.997	0.525	0.375–0.736	0.457	0.318–0.657
1991–92	4,286	1.000	1.000–1.000	0.482	0.269–0.863	0.482	0.269–0.864
Pooled	34,325	0.854	0.786–0.927	0.646	0.556–0.752	0.552	0.464–0.656

^a Summer includes May through November; winter includes December through April.

^b Survival rates calculated using methods described by Heisey and Fuller (1985).

large increase in size could have included production of multiple litters, immigration, or that we underestimated pack size during winter 1990–91. Spring and autumn wolf populations exhibited similar trends during the study period (Table 4). Extrapolation of wolf densities within the study area to all of northwest Alaska (119,140 km²) suggested that during the study, wolf numbers varied from about 786 in autumn 1989 (postdenning) to 179 in spring 1991 (predenning).

Survival

We found no differences in annual survival rates by sex ($X^2 = 1.0$), age ($X^2 = 1.0$), year ($X^2 = 1.3$), or their interaction (both weighted and unweighted) based on numbers of radio days (Table 5). However, because of small sample sizes, our power to detect differences was low. The relatively low survival rates during 1990–91 and 1991–92 (i.e., 0.457 and 0.482, respectively) appeared to be the result of high human harvest and a rabies epizootic (see Mortality). During other years when rabies was not a significant source of mortality, annual survival rates ranged from 0.585 to 0.654 (Table 5). Although 34 pups were radio collared during the study, most (88%) were captured during March and April (Appendix); consequently, we were unable to estimate pup survival rates.

For all wolves, annual survival rates averaged 0.552 (Table 5). Survival was greatest ($Z = 3.4$, $P < 0.005$) during summer months (0.854) and was lower during win-

ter (0.646) due largely to harvest mortality ($Z = 5.9$, $P < 0.005$). Weather conditions in northwest Alaska precluded hunting from snowmobile during autumn and early winter due to inadequate snow cover and extreme winter temperatures. In February, snow depths were sufficient for snowmobile 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 sign. Wolf hunting has been a traditional practice among Inupiat Eskimos. With the relatively recent acquisition of snowmobiles, 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, 42pp., 1989).

The overall annual survival rate of wolves (0.552) was slightly lower than that found in several areas of North America. Peterson *et al.* (1984) reported an annual survival rate of 0.67 on the Kenai Peninsula, Alaska, and Fuller (1989) reported a rate of 0.64 for north-central Minnesota. However, 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; these values were considered to be indicative of heavily exploited wolf populations. Prior to the rabies epizootic in 1990–91, annual survival rates ranged from 0.585 to 0.654, and the wolf population increased. Survival rates were low (0.457–0.482) during

Table 6. Fates of 86 radio-collared wolves and cause-specific mortality rates in northwest Alaska, April 1987 through May 1992^{a,b}.

Year ^c	As of 30 May 1992			Hunting			Wolf predation	Rabies	Old age	Total
	Alive	Missing	Fate unknown	Snowmobile	Aircraft	Starvation				
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	7	1	25
1990–91	3	9	0	11	0	3	0	4	0	30
1991–92	4	3	2	6	0	0	0	0	0	15
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
Cause-specific mortality rate				0.301	0.022	0.033	0.007	0.079	0.007	0.448

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

^b Cause-specific mortality rates per year were calculated using methods described by Heisey and Fuller (1985).

^c Biological year: 1 Jun–31 May.

1990–91 and 1991–92 (Table 5), and the wolf population declined. Also, our annual survival rate estimates may have been too high because pups were not radio tracked in much of the winter when they 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 were unable to detect significant differences in survival rates between dispersers (0.564) and nondispersers (0.518). Fuller (1989) in Minnesota and Hayes et al. (1991) in the southern Yukon Territory reported results similar to ours.

Mortality

The causes of mortality of radio-collared wolves were classified as snowmobile-assisted hunting, aircraft-assisted hunting (also referred to as "land and shoot trapping"), starvation, wolf predation, rabies, or old age. Of the 86 wolves radio collared, 53 were dead by May 1992 (Table 6).

Hunting was the largest cause of death ($n = 36$) accounting for 69% of known mortalities and resulted in an overall mortality rate of 0.32 (Table 6). Of those mortalities, 96% were taken by snowmobile-assisted hunters and the remainder by aircraft-assisted hunters. None of the radio-

collared wolves was trapped. Rabies was the second largest cause of death (21%) and the most important cause during summer, particularly during 1989–90. Other natural causes of death included starvation ($n = 3$), wolf predation ($n = 1$), and old age ($n = 1$).

Most (63%) mortalities occurred during December through April (Table 7); hunting accounted for 89% of the mortalities. Annual cause-specific mortality rates ranged from 0.16 to 0.52. Rabies also was a significant cause (21% of mortalities; 0.08 cause-specific mortality rate) of mortality with 91% of rabies deaths occurring during May through September. The relatively high incidence of rabies-caused mortality during 1989–90 (i.e., 0.19 cause-specific mortality) was a significant factor in causing the wolf population to decline. Wolf populations are usually higher in autumn than during spring due to reproduction. However, during this study wolf density declined from 4.4 to 4.2/1,000 km² from spring to autumn 1990, respectively. Even though mortality the previous winter was low (i.e., hunting cause-specific mortality rate of 0.16), relative to other years (i.e., hunting cause-specific mortality rates ranging from 0.34 to 0.52), the impact of rabies on the wolf population was to greatly diminish the capacity of the population to rebound.

Hunting and Trapping.—During 1985–

Table 7. Timing and causes of mortality or month that radio contact was lost for radio-collared wolves in northwest Alaska, April 1987 through April 1992^a.

Month	Hunting				Wolf predation	Total known deaths		Missing ^b		Total		
	Snowmobile	Aircraft	Rabies	Starved		Old age	n	%	n	%	n	%
May	1	0	6	0	0	0	7	13.5	6	25.0	13	17.1
Jun	0	0	1	0	0	1	2	3.8	1	4.2	3	3.9
Jul	0	0	1	0	0	0	1	1.9	5	20.8	6	7.9
Aug	0	0	1	0	0	0	1	1.9	3	12.5	4	5.3
Sep	0	0	1	0	1	0	2	3.8	1	4.2	3	3.9
Oct	0	0	0	0	0	0	0	0	3	12.5	3	3.9
Nov	1	0	0	0	0	0	1	1.9	0	0	1	1.3
Dec	5	0	1	0	0	0	6	11.5	0	0	6	7.9
Jan	6	0	0	1	0	0	7	13.5	0	0	7	9.2
Feb	5	2	0	0	0	0	7	13.5	1	4.2	8	10.5
Mar	14	0	0	2	0	0	16	30.8	2	8.3	18	23.7
Apr	2	0	0	0	0	0	2	3.8	2	8.3	4	5.3
Total	34	2	11	3	1	1	52	99.9	24	100.0	76	99.9

^a Excludes 1 sacrificed wolf.

^b Suspected dead or dropped collar counted as missing.

86 through 1991–92, an average of 60 wolves ($n = 417$, range = 18–93) was reportedly killed by hunters and trappers within northwest Alaska (Table 8). Snowmobile-assisted hunters and trappers accounted for 64% of the human harvest whereas 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; the latter animals were either trapped or snared after aircraft was 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 snowmobiles was the most common method of harvest.

Reported harvest dates indicated that most wolves (54%) were harvested during March and April (Alas. Dep. Fish and Game, Kotzebue) 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 7).

Reported sex ratios within the harvest ($M = 306$, $F = 210$) were significantly skewed towards males ($X^2 = 18.4$, 1 df, $P < 0.001$). Although harvest chronology and sex ratio data were similar to those provided by radio-collared wolves (in which males were selected), total reported

Table 8. Summary by month and year of wolf harvests in northwest Alaska, 1985–86 through 1991–92, according to sealing records (Alas. Dep. Fish and Game files, Kotzebue).

Month	1985–86	1986–87	1987–88	1988–89	1989–90	1990–91	1991–92	Total	%
Sep			2		4	6	7	21	5.4
Oct	0	0	0	2	0	0	0	0	0
Nov	0	0	1	0	14	2	1	22	5.7
Dec	3	0	3	1	15	5	4	47	12.1
Jan	1	1	15	18	4	4	4	42	10.8
Feb	2	0	13	13	2	20	5	56	14.4
Mar	0	4	45	12	15	5	28	152	39.1
Apr	10	20	13	29	6		6	44	11.3
Unknown	2	9	1	8	2	1	1	5	1.3
Total	18	34	93	83 ^a	62 ^b	43	56	389	100.1

^a At least 10 additional wolves were killed but not sealed.

^b Eighty reported harvested of which 27 were taken illegally and the date of kill for 18 was unknown.

annual harvests were quite low in relation to actual harvests. Wolf population density within the study area was estimated for spring and autumn (Table 4) and compared to annual reported harvests. Assuming that most losses from radio-marked packs during autumn through spring were related to hunting and trapping mortality, these data suggested that only 14–70% of the annual harvests are reported. Virtually all state annual survey-inventory reports have indicated that compliance with sealing requirements in northwest Alaska is low (Larsen and James 1987, 1988; Dau 1989a,b), and consequently reported harvests are not representative of actual mortality within the wolf population.

Allowable Mortality Rates.—We examined the relationship between annual mortality and exponential rates of increase (r) (Caughley 1978) for large (≥ 7) and small (≤ 6) wolf packs. The 2 variables were not correlated for small packs (Fig. 6A), but were inversely correlated for large packs (Fig. 6B). Although there was no difference in the slopes of the 2 regressions ($F = 0.08$, $P = 0.78$), suggesting that both pack types responded similarly to overwinter mortality, small packs had greater rates of increase ($F = 5.33$, $P = 0.03$) than large packs for a specific rate of mortality. Small packs that contain at least 1 breeding female may be able to compensate for high mortality because of high reproduction potential. Usually only 1 female/pack reproduces and unless multiple litters occur, large packs cannot compensate for as high a mortality rate as small packs.

Based on 9 studies in North America, Fuller (1989) indicated that wolf populations remained stable when overall mortality rates were 35% and human-caused mortality rates were 28% (Table 9). Mortality rates and rates of increase for both small and large packs combined in this study were inversely correlated ($r_s = -0.60$, $P = 0.002$) and indicated that on average, each pack would remain stable when winter mortality equaled about 53% (Fig. 6C). One potential problem with estimating sustainable mortality rates based upon individual packs is that the number

and the sex and age structure of the pack also 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 also 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) also can have a significant impact on rates of increase and sustainable mortality rates. It is clear that the amount of mortality that individual wolf populations can withstand varies by population and depends on a number of factors.

Feeding Ecology

During April 1987 through July 1992, we observed 19 radio-marked wolf packs at 184 prey carcasses; 90% were ungulates. Because all of the observations were made from fixed-wing aircraft, these values underrepresent the importance of smaller prey such as snowshoe hares, muskrats, and 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 carcasses. Caribou and moose composed 51 and 42% of the observed kills, respectively (Table 10). Adult (>2 yr) caribou (38%) and adult moose (25%) were the most frequently killed prey. They also were the most frequent age class scavenged (3 ad moose and 3 ad caribou out of 16 carcasses). 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 Distribution and Abundance of Caribou) and lack of detection of kills as a result of infrequent relocation of radio-marked wolf packs.

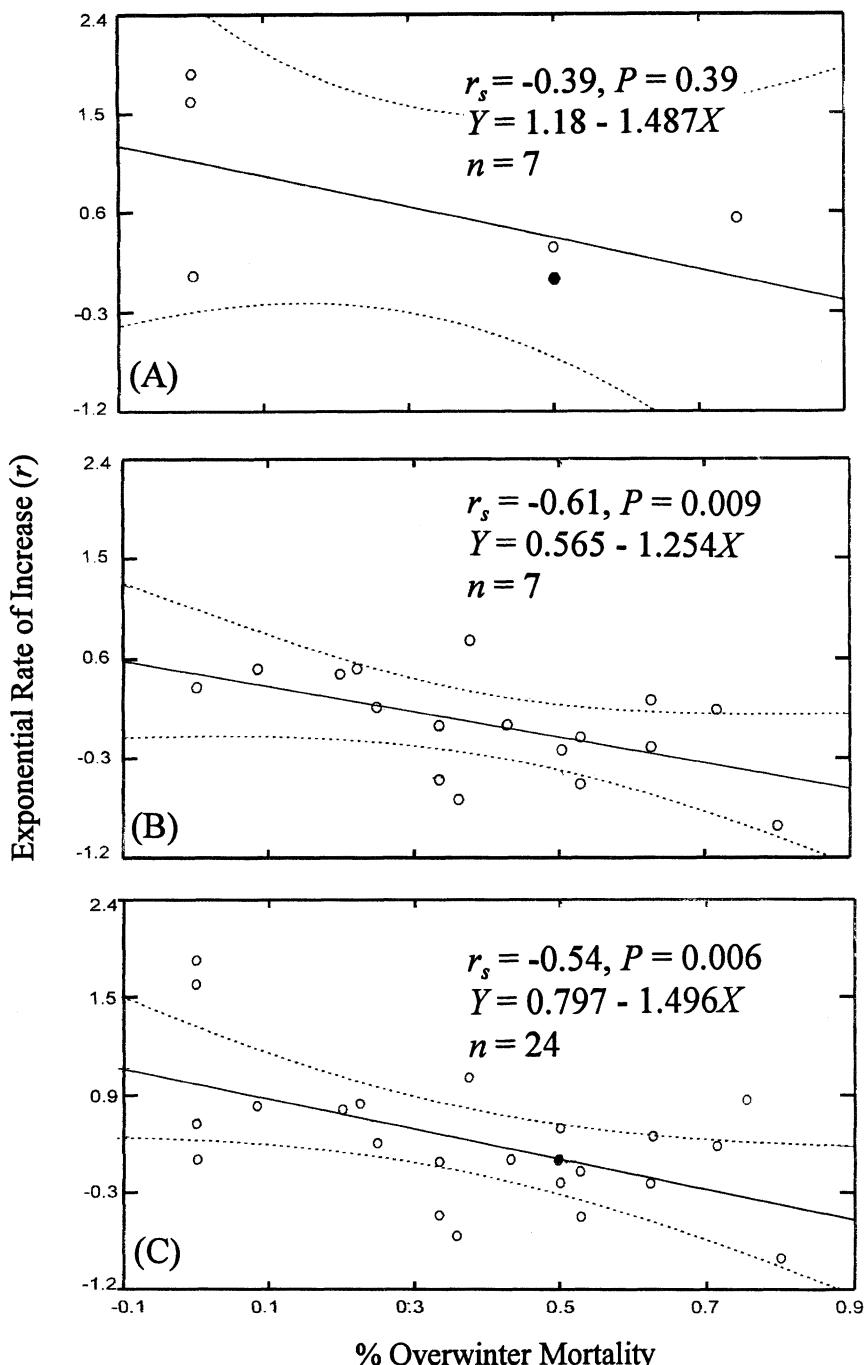


Fig. 6. Comparison of annual rates of mortality per wolf pack (autumn to spring) to exponential rates of increase (r from autumn to autumn) for small (A; ≤ 6 individuals), large (B; > 7 individuals), and all (C) radio-marked wolf packs in northwestern Alaska, autumn 1987 through autumn 1991. Dotted lines indicate 95% confidence interval of predicted mean Y-value whereas dark points indicate 2 data points.

Table 9. 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. yrs	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 al. 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	0.45	0.32	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 1985 ^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 $r_s = -0.87$, 8 df, $P < 0.001$. Correlation between exponential rate of increase and annual human-caused mortality rate; weighted $r_s = -0.99$, 8 df, $P < 0.001$.

^b Mortality rate of early winter population; assumes summer survival of adults = 1.00.

^c Minimum mortality rate because only includes human-caused mortality.

^d Recalculated.

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 the entire wolf study area, aerial surveys over the area allowed us to compare the age composition of wolf kills with those observed in the prey population.

Wolves killed proportionately more adult and fewer caribou calves (9–11 months old) than expected based upon

spring caribou counts conducted during 1987 through 1990 (Machida 1992) ($X^2 = 15.1$, 1 df, $P = 0.0001$). Also, wolves killed more adult caribou and relatively fewer caribou calves during winter, although our analysis could be biased because there may have been a lower proportion of caribou calves within the study area during winter than in the caribou population as a whole. Ballard et al. (1987) and Mech et al. (1995), however, also reported a relatively low incidence of calf caribou being killed by wolves in winter.

Table 10. Wolf kills (excludes scavenging) observed while monitoring radio-marked wolf packs in northwest Alaska, April 1987 through July 1992.

Months	Moose				Caribou					Total
	Calf	Yearling	Adult	Unclassified	Calf	Yearling	Adult	Unclassified	Unidentified	
May	2		1		2		3	1		9
Jun	2		1				1		1	5
Jul		1							1	2
Aug			1		1		3	1		6
Sep										0
Oct	1	2	2				5		2	15
Nov			1		2			1	1	5
Dec			1					1		2
Jan	1						4	2		7
Feb	1						1			2
Mar	4	1	15		1	1	12	1	1	36
Apr	6	4	20	4	2	3	35	2	3	79
Total	17	8	42	4	3	9	64	9	8	168
%	10.1	4.8	25.0	2.4	1.8	5.4	38.1	5.4	4.8	100.2

Sex-age composition surveys of moose were conducted in the Tagagawik River (located just west of the study area) during autumns 1987 through 1989 and in 1992 (J. R. Dau, Alas. Dep. Fish and Game, Kotzebue, pers. commun.). We used the sum of these counts to calculate expected calf:adult ratios. Calf moose composed 17% of the moose observed during autumn counts ($n = 1,487$) and 21% of the kills. We were unable to detect differences in age ratios of moose killed by wolves in comparison to calf:adult moose ratios in autumn ($X^2 = 1.09$, 1 df, $P = 0.30$). This lack of selectivity for calves differs from that found elsewhere in Alaska and Canada.

Fuller and Keith (1980), Gasaway *et al.* (1983), Peterson *et al.* (1984), 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 these studies and our study was that caribou was the primary prey species in this study, whereas moose was the primary prey in the others. In addition, poor body condition of some moose may have made them more vulnerable to wolf predation. Based on marrow fat values, we concluded that wolves were preying upon caribou in good condition and upon moose that were in marginal condition (see Age and Physical Condition of Ungulate Prey). If we assume that adult and calf moose were equally vulnerable, or nearly so, to wolf predation due to deep snow and marginal body condition, this may explain why wolves did not disproportionately select moose calves.

Distribution and Abundance of Caribou

The percentage of radio-collared caribou occurring within the study area during January through April each year declined from 21% in 1988 to 6% in 1989 to 3% in 1990 (Table 11). Our incidental observations of numbers of caribou observed during radio-tracking flights during these months followed the same trend. During April of each year, the percentage of radio-

Table 11. Occurrence of radio-collared caribou from the Western Arctic Herd within or ≤ 80 km from the northwest Alaska wolf study area, during winter and early spring 1988 through 1990.

Year	No. of radio-collared caribou	Date	% of caribou within area
1988	104	20 Jan	2.9
		3 Feb	1.0
		8 Feb	10.6
		16 Mar	45.2
		16–25 Apr	44.2
		\bar{x}	20.8
1989	92	22 Feb	5.4
		11 Mar	0
		20 Mar	1.1
		22 Mar	5.4
		27 Mar	2.2
		30–31 Mar	6.5
		3–5 Apr	19.6
1990	127	\bar{x}	5.7
		28 Jan	2.4
		19 Feb	0
		23 Mar	3.9
		6–9 Apr	3.1
		19–20 Apr	4.7
		\bar{x}	2.8

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.

Kill Rates

Between 11 March and 28 April during 1988 through 1990, we relocated 3–6 (total = 13) wolf packs (ranging in size from 1 to 23 individuals) each day (Table 12). 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 per capita kill rates. Messier (1985) and Dale *et al.* (1995) described this number as “traveling pack size.” Thirteen packs were observed on 68 carcasses during the intensive study period. Seven carcasses (10.3%) were scavenged and not killed. These animals could have been killed by

Table 12. Dates monitored and number of prey killed and scavenged by 6 radio-marked wolf packs that were relocated and backtracked daily in northwest Alaska, 1988–90.

Year	Pack name	Traveling pack size ^a	Dates monitored	Caribou					Moose					Known scavenged ungulate Total	
				Yearling Calf	Ad F	Ad M	Ad un-known ^b	Total	Yearling Calf	Ad F	Ad M	Ad un-known ^b	Total		
1988	Jade Mt.	1	31 Mar–21 Apr	0	1	0	0	0	0	0	0	0	0	2	3
	Purcell Mt.	9	1–28 Apr	0	0	4	2	2	0	0	0	1	0	0	9
	Rabbit Mt.	2	31 Mar–28 Apr	1	1	0	0	1	0	0	0	0	0	2	5
1989	Ingruksukruk	4	11 Mar–1 Apr	0	0	0	0	1	0	0	0	1	3	3	8
	Nuna Creek	13	12 Mar–5 Apr	0	0	0	0	0	1	0	2	2	1	0	6
	Purcell Mt.	13	11 Mar–1 Apr	0	0	0	0	1	1	0	1	1	2	0	6
1990	Rabbit Mt.	2	11 Mar–5 Apr	0	0	0	0	0	0	0	1	1	0	0	2
	Dunes	5	21–27 Mar	0	0	0	0	0	1	0	0	0	1	0	2
	Dunes	5	6–22 Apr	0	0	0	0	0	2	0	0	0	3	0	5
	Ingruksukruk	4	8–20 Apr	0	2	0	0	1	0	0	0	0	0	0	3
	Nuna Creek	23	23–27 Mar	0	0	0	0	0	1	0	0	0	0	0	1
	Nuna Creek	19	5–19 Apr	0	0	0	0	1	1	0	0	0	4	0	6
	Purcell Mt.	11	6–20 Apr	1	0	1	1	7	1	0	0	0	1	0	12
	Total			2	4	5	3	14	8	0	4	6	15	7	68

^a As defined by Messier (1985) and Dale et al. (1995).

^b Assumed to be adult females for all future calculations.

wolves prior to the intensive relocation effort.

Adult caribou (41%), adult moose (36%), and calf moose (13%) composed the observed kills (Table 12). Smaller packs ($n = 3$) comprised of 1–4 individuals were responsible for all of the observed scavenging (7 carcasses). Three cases of multiple kills were observed, and thus numbers of ungulates killed per successful attack averaged 1.2 ± 0.1 ($n = 54$). 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. 1995). Dale et al. (1995) 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 13). Average pack size was 8.5 ± 1.8 . We failed to relocate wolf packs an average of 1.2 ± 0.3 days/pack during the intensive study period (Table 13) due to

inclement weather. Therefore, estimated kill rates should be viewed as minimal. Ungulate kills averaged 4.6/wolf/100 days (range 0.7–7.8; 2.4 moose and 2.2 caribou/wolf/100 days, respectively), and the average time interval between ungulate kills for packs was 3.8 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 $53 \pm 3.1\%$ had been consumed ($n = 75$; note that 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 upward). When each kill was last observed, consumption was estimated at $91 \pm 2.1\%$ ($n = 53$).

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 Crête 1985, Ballard et al. 1987) investigators have assumed that all available prey biomass (75% of prey weight) was available to wolves for con-

Table 13. Kilograms consumed, kill rate, and time intervals between ungulate kills for 6 radio-marked wolf packs that were relocated and backtracked daily to previous locations during late winter and early spring in northwest Alaska, 1988–90.

Year	Pack name	Pack size		No. days		Kg prey available/wolf/day ^c	Kg prey consumed (no. ungulates/wolf/day ^d)	Kill rate (kg/gululates/wolf/100 days)	Time interval between ungulate kills ^e (days/kill)
		Traveling ^a	Range	Monitored ^b	Missed				
1988	Jade Mt.	1	1	21	0	80.8	3.8	0.09	4.8
	Purcell Mt.	9	1–11	27	2	900.4	3.7	0.09	3.7
	Rabbit Mt.	2	1–2	28	1	173.1	3.1	0.07	5.4
1989	Ingruksukruk	4	1–9	21	2	1,340.4	16.0	0.37	6.0
	Nuna Creek	13	9–15	24	1	1,693.5	5.4	0.13	1.9
	Purcell Mt.	13	9–14	21	0	1,419.1	5.2	0.12	2.2
1990	Rabbit Mt.	2	1–2	25	1	640.5	12.8	0.30	4.0
	Dunes	5	1–5	6	1	412.5	13.8	0.32	6.7
	Dunes	5	2–5	16	3	1,125.0	14.1	0.33	7.8
	Ingruksukruk	4	3–6	12	2	182.7	3.8	0.07	6.3
	Nuna Creek	23	23–24	6	0	112.5	0.8	0.02	0.7
	Nuna Creek	19	15–23	13	1	1,378.3	5.6	0.13	2.4
	Purcell Mt.	11	5–13	14	1	1,057.3	6.9	0.16	7.8
	Total			234	15				
	\bar{x}	8.5	5.5–10.0	18.0	1.2	809.0	5.3	0.12	4.6

^a As defined by Messier (1985) and Dale et al. (1995).

^b Excludes first day relocated.

^c Assumes male, female, yearling, and calf caribou weight at 96, 76, 67, and 36 kg (J. L. Davis, Alas. Dep. Fish and Game, Fairbanks, pers. commun.), respectively, with percent consumable equal to 85, 87, 87, and 95% (Sumanik 1987), respectively. Yearling caribou weight was estimated from relationship of calf caribou to calf and yearling moose. Adult male, adult female, yearling, and calf moose were assumed to weigh 454, 400, 278, and 150 kg, respectively (Franzmann et al. 1978, Hayes et al. 1991), and 75% was assumed consumable (Peterson 1977, Ballard et al. 1987, Sumanik 1987). We assumed scavenged carcasses had 15 kg of prey available and that 75% were consumed.

^d Used mean mass of all captured wolves.

^e Excludes scavenged kills.

sumption. 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 (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 a 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 might 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 in this study was 3.7 ± 0.8 ($n = 66$; range = 0–30). Excluding 2 observations where 30 ravens were present caused the average number to decline to 2.7 ± 0.5 . 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. Bal-

lard, co-author, 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 decision, Hayes et al.'s (1991) point of considering scavenging activity in wolf consumption rates warrants further investigation.

Messier and Crête (1985) indicated that wolf kill and consumption rates were high in areas with higher densities of moose. Fuller (1989) examined relationships between ungulate biomass indices (assigns biomass values to different sized prey species; see Table 14) 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 166 moose/1,000 km² based on census data,

Table 14. Ungulate biomass index per wolf versus estimated winter consumption rates of ungulates by wolves during winter in North America (modified from Fuller 1989)^a.

Location	Major prey species	Ungulate biomass index/wolf	\bar{x} mass of wolf (kg)	Consumption rate in winter		Reference
				kg/wolf/day	kg/kg of wolf/day	
East-central Ont.	Deer	112	30	2.9	0.10	Kolenosky 1972
Northern Alta.	Bison	152	38	5.3	0.14	Oosenbrug and Carbyn 1982
West-central Yukon	Sheep	153	37	3.0	0.08	Sumanik 1987
North-central Minn.	Deer	161	34	2.0	0.06	Fuller 1989
Southwest Que.	Moose	162	30	2.2	0.07	Messier and Crête 1985
Northeast Minn.	Deer	178	30	2.9	0.10	Mech 1977
Isle Royale, Mich.	Moose	225	33	7.2	0.22	Peterson 1977
Northeast Alta.	Moose	231	38	5.5	0.14	Fuller and Keith 1980
Isle Royale, Mich.	Moose	264	33	4.9	0.15	Peterson and Page 1988
Northwest Alas.	Caribou; moose	267	43	5.3	0.12	This study
Denali Park, Alas.	Moose	334	40	4.5	0.11	Haber 1977
Southwest Manit.	Elk	336	32	6.8	0.21	Carbyn 1983
Kenai Peninsula, Alas.	Moose	345	40	4.8	0.12	Peterson et al. 1984
Northwest Minn.	Deer	400	32	2.9	0.09	Fritts and Mech 1981
South-central Alas.	Moose	659	40	7.1	0.18	Ballard et al. 1987

^a Bison (*Bison bison*), moose, elk, bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), mule deer, and white-tailed deer assigned relative biomass values of 8, 6, 3, 2, 1, 1, and 1, respectively.

and arbitrarily assumed a minimum of 2,000 caribou (i.e., 164/1,000 km²) within the area on a year-round basis, we derived a minimum biomass index of 267/wolf (Table 14). We assumed that the captured wolves were representative of the wolf population and had an average weight of 43 ± 0.5 kg for calculating consumption rates during the intensive study period (cf. Table 1). Each wolf had 5.3 kg of ungulate prey per day or 0.12 kg/kg wolf/day (Table 13). 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 between new kills 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 15). 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 Crête (1985), Ballard et al. (1987), and Hayes et al. (1991) reported that small packs remained with adult moose kills longer than large packs. Although we found no correlation between pack size and length of stay at either adult moose ($r_s = -0.28$, $n = 21$, $P = 0.22$) or adult caribou kills ($r_s = 0.07$, $n = 15$, $P = 0.79$), 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 be related to 2 factors. Firstly, caribou from the WACH weigh less than caribou from the Nelchina Caribou Herd (Skoog 1968; J. Dau, Alas. Dep. Fish and Game, Kotzebue, pers. commun.). Secondly, in the Nelchina study, Ballard et al.

Table 15. Average number of days spent at ungulate kills by 6 radio-marked wolf packs during late winter and early spring in northwest Alaska, 1988–90^a.

Year	Pack	Moose kills												Caribou kills											
		Calf		Yearling		Ad F		Ad M		2 Ad ^c		Calf		Yearling		Ad F		Ad M		Ad F and calf		7 Ad ^c			
		Days	n ^b	Days	n	Days	n	Days	n	Days	n	Days	n	Days	n	Days	n	Days	n	Days	n	Days	n	Days	n
1988	Jade Mt.	1		1	1							1	1	1	1	1	1	1.2	6	1.5	2				
	Purcell Mt.	9																1	1	1	1				
	Rabbit Mt.	2																							
1989	Ingruksukruk	4																							
	Nuna Creek	13																							
	Purcell Mt.	13																							
	Rabbit Mt.	2																							
1990	Dunes	5	1	1	1	1	1	1	1	2	1														
	Dunes	5	1	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 ^d	1	3	1	1	2.0	16	1.8	5	2	1	1	1	3	1.1	12	1.7	3	1	1	1	1	1	

^a Assumes unclassified moose and caribou were adult females.^b Number of observations.^c Multiple kill.^d Arithmetic mean.

(1987) located wolves every other day. They assumed that if >50% of a kill was consumed 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 16). 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 ($r_s = -0.45, n = 19, P = 0.06$) or adult caribou ($r_s = -0.03, n = 12, P = 0.92$). 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 (Peterson 1977, Messier and Crête 1985, Ballard et al. 1987, Sumanik 1987, Dale et al. 1995). However, Haber (1977) and Hayes et al. (1991) found no correlation between pack size and kill rate, but Hayes et al. (1991) had a relatively large number of pairs and no large packs. We examined the relationships between pack size and ungulate kills/wolf/day, time intervals between ungulate kills, and prey weight/wolf/day. Pack size and ungulate kills/wolf/day and prey weight/wolf/day were not correlated ($r_s = -0.50, n = 13, P = 0.08$ and $r_s = -0.13, n = 13, P = 0.67$, respectively), but interval between kills was negatively correlated ($r_s = -0.58, n = 13, P = 0.04$). 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. 1995, this study) to further explore these relationships. With this expanded data set, wolf pack sizes and prey weight/wolf/day (Fig. 7) was negatively correlated, but pack size and ungulate kills/wolf/day was not (Fig. 8). Messier (1994) did not find an independent effect

of pack size on killing rate. Larger packs may be able to kill more prey than smaller packs but the kills must be shared among a greater number of individuals. Consequently, per capita killing rate may be little influenced by pack size after controlling for the effects of ungulate density (Messier 1994), which was not done in this study.

Our data suggest that wolves select caribou when they are available. Wolves switched prey species as a result of changes in caribou distribution during the study (Tables 12, 13). 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 composed 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. Proportionately more caribou were killed in 1988 when they were more abundant in the study area than in 1989 ($\chi^2 = 11.3, 1 \text{ df}, P < 0.001$) or 1990 ($\chi^2 = 14.3, 1 \text{ df}, P < 0.001$) when they were less abundant. There were no differences in the proportions of caribou killed in 1989 and 1990 ($\chi^2 = 0.03, 1 \text{ df}, P = 0.87$). Dale et al. (1995) 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, were likely 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*

Table 16. Time interval in days between ungulate kills for 6 radio-marked wolf packs in northwest Alaska during late winter and early spring, 1988–90.

Year	Pack	Name	Size	Moose kills						Caribou kills									
				Calf		Yearling		Ad F		Ad M		Calf		Yearling		Ad F			
				Days	n ^b	Days	n	Days	n	Days	n	Days	n	Days	n	Days	n		
1988	Jade Mt.	1				2	1					2	1			1.8	6		
	Purcell Mt.	9													6	1	1		
	Rabbit Mt.	2													3	1			
	Ingrukukruk	4				5.3	1												
	Nuna Creek	13				6.3	3	2.5	2										
	Purcell Mt.	13				4.7	3	3	1						1	1			
1989	Rabbit Mt.	2																	
	Dunes	5				3	1												
	Dunes	5				4	1	3	1										
	Ingrukukruk	4																	
	Nuna Creek	19				3	1			2	4								
	Purcell Mt.	11																	
Weighted \bar{x}				7.3 ^d	3.5	2	3	1	4.0	14	3.2	5	3	1	1	5.0	3	1.8	10
																	5.5	2	
																	1	3	
																	1	1	

^a Assumes unclassified moose and caribou were adult females.^b Number of observations.^c Multiple kill.^d Arithmetic mean.

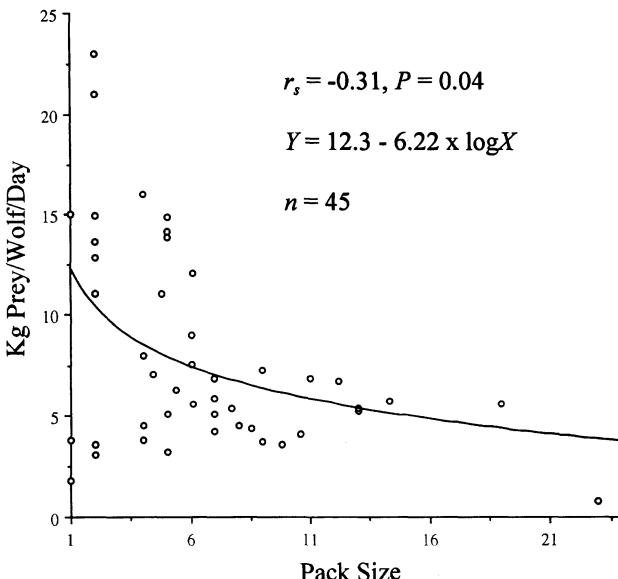


Fig. 7. Comparison of wolf pack sizes and kilograms of prey weight available/wolf/day from several study areas in North America where caribou and moose were the principal prey species. Studies used in calculations were Ballard et al. (1987) from south-central Alaska, Hayes et al. (1991) from the Yukon Territory, Dale et al. (1995) from Gates of the Arctic National Park, Alaska, and this study in northwest Alaska. Data sets were collected during March and April.

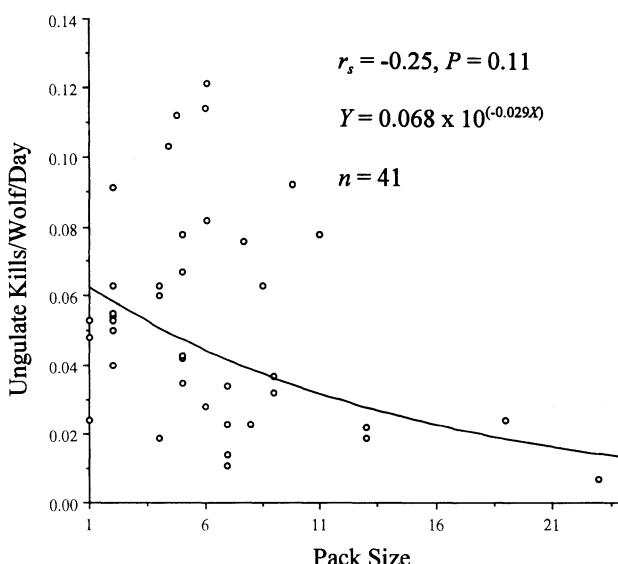


Fig. 8. Comparison of wolf pack sizes and number of ungulate kills/wolf/day from several study areas in North America where caribou and moose were the principal prey species. Studies used in calculations were Ballard et al. (1987) from south-central Alaska, Hayes et al. (1991) from the Yukon Territory, Dale et al. (1995) from Gates of the Arctic National Park, Alaska, and this study in northwest Alaska. Data sets were collected during March and April.

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. In this study, wolves appeared to switch to moose when caribou were no longer available. We suggest there is a threshold density of caribou below the 200/1,000 km² reported by Dale et al. (1995) where wolves switch to more available prey in spite of a preference for caribou.

Dale et al. (1995) 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 km², respectively. The number of moose and caribou killed by wolves during March within individual territories averaged 0.8 ± 0.4 and 13.4 ± 1.1 , respectively. Although we did not determine prey densities within pack territories, we observed 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 within the study area did not mean they were necessarily within the pack territories we studied.

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 may be explained by the lack of 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 Leuth 1966, Neiland 1970, Franzmann and Arneson 1976, Pe-

terson 1977, Peterson et al. 1984, Ballard et al. 1987, Mech et al. 1995). However, as pointed out by both Mech and Delgiudice (1985) and Ballard et al. (1987), statements about the 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.

Adult caribou killed by wolves during 1989 had an average femur fat level of $79 \pm 6\%$ ($n = 10$). 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.

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). Mech et al. (1995) 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. Based on their criteria, we concluded that during this study wolves preyed upon caribou that had relatively high (8 of 13 with $>87\%$ fat) marrow fat values in late winter and may have been in good condition whereas most moose (2 of 10 with $>87\%$ fat) were probably in marginal condition in late winter.

EFFECTS OF WOLF PREDATION ON WESTERN ARCTIC CARIBOU HERD AND MOOSE Effects on Caribou

Most calf mortality in caribou and moose occurs during the first month of life

(Franzmann et al. 1980, Ballard et al. 1981b, Whitten et al. 1992, Adams et al. 1995). Barren-ground caribou, unlike other ungulates, attempt to escape predators by giving birth 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 1964–66. Low recruitment coupled with heavy human harvests were thought to have initiated a population decline in that herd (Van Ballenberghe 1985, 1989; Bergerud and Ballard 1988, 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 a size of 417,000 in 1992 from a low of about 75,000 in 1976.

The total range of the WACH has been estimated at 362,600 km² (Davis et al. 1980). Extrapolation of average autumn wolf densities observed in this study (4.8/1,000 km²) to the total range of the WACH yields a gross autumn wolf population estimate of 1,740 wolves. Although other areas within the WACH range apparently have higher wolf densities (i.e., 7.4/1,000 km² in Gates of the Arctic National Park [Adams and Stephenson 1986] and 8.4/1,000 km² 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 cari-

bou equivalents annually in the WACH. This estimate suggests about 6–7% of the caribou population in 1992 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 1970's, excessive hunting and wolf predation were thought to be the major causes (Davis and Valkenburg 1985). Reports of caribou harvest were 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 >2,000/1,000 km² (Bergerud 1983, Skoglund 1985). Current WACH densities are about 1,149/1,000 km² (Machida 1992) with wolf densities ranging from 4.8 to 8.4/1,000 km² (Spindler 1992, Dale et al. 1995, 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 1970's, wolf predation could become a significant source of mortality. Continuation of censuses every 2–3 years should alert managers when a decline is in progress. Reductions in human harvest also would 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 theoretical wolf density for northwest Alaska would be about 16.4 wolves/1,000 km² (assumed 1,149 caribou/1,000 km² and 200 moose/1,000 km²) if no other prey species were available and if wolves migrated with caribou. However, if we assumed 166 moose/1,000 km² based on census data and arbitrarily assumed a

minimum of 2,000 caribou (i.e., 164/1,000 km²) within the study area on a year-round basis, the predicted wolf density would be about 8.2 wolves/1,000 km². 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 km². Because northwest Alaska has moderate to low moose densities, wolf densities could probably be higher than 6.5/1,000 km² 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, Kotzebue, 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 might 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 would be 1 option that might contribute to that effort. However, allowing wolf densities to increase could change the effects of predation on resident moose populations.

Effects on Moose

Prior to initiation of this study, historical reports and conventional wisdom suggest-

ed 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. (1995) 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 may do so in response to a lack of prey within their territory. Such movements do not occur annually and are not predictable from year to year, unless prey numbers are known.

Prior to the 1940's, there were few, if any, moose within northwest Alaska (J. R. Dau and L. A. Ayres, Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 24pp., 1993). Dau and Ayres indicated that during the late 1940's and early 1950's moose colonized northwest Alaska. The moose population grew through the mid-to-late 1980's. 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, they 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. 1989) 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 Brooks Mountain Range 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, Kotzebue, 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." 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 Crête (1985), and Gasaway et al. (1992) indicated that moose occur at densities <400/1,000 km² when wolves are present and uncontrolled. When predator densities are greatly reduced, moose attain densities of 2,000–4,000/1,000 km². Prior to the establishment of resident moose populations, wolves may have migrated with caribou or

may have existed at relatively low densities due to lack of alternate prey.

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 12; 1989 data and multiple kills of caribou were excluded). During the remainder of the year, moose composed 46% (Table 10) of the wolf ungulate 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 km² (Larsen et al. 1986). Assuming a wolf consumption rate of 5.3 kg/wolf/day, wolves would kill 216–295 moose (Ad F moose equivalents) per year or 11–14% of the moose population annually. In some areas, sheep also may experience relatively high rates of mortality due to wolf predation. These estimates of mortality due to wolves combined with unreported human harvests of moose and sheep and with severe winter conditions could cause moose and sheep densities to decline in northwest Alaska. Dau and Ayres (Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 24pp., 1993) recently reported that 20 of 45 adult moose radio collared in the Noatak River drainage during April 1992 died during 1992–93 and that 9 (20% over a 2-yr period) 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. 1981b, Ballard and Larsen 1987, 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. (1993) 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. (1993) 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 and during severe winters, could be 1 cause of the apparent moose decline reported by Dau and Ayres (Noatak River moose radio telemetry project progress report, Alas. Dep. Fish and Game, Kotzebue, 24pp., 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 would almost certainly be reduced during years that caribou are unavailable to wolves as winter prey. Messier (1994: 485) indicated that relatively little information exists on the influence of alternate prey on moose–wolf relationships but that the relative vulnerability of the primary versus the alternate prey to predation plays a determining role in creating either a diluting or exacerbating impact on the abundance of the primary prey. In our case, when caribou are present they dilute the effects of wolf predation on moose, which may allow for a greater abundance of moose than otherwise would be expected. When caribou are absent, wolf predation may have a relatively greater impact on moose, and moose densities would be lower than when alternate prey exist.

CONCLUSIONS

1. Winter territories ($\bar{x} = 1,372 \text{ km}^2$) were significantly ($P = 0.001$) larger than summer territories ($\bar{x} = 621 \text{ km}^2$), but summer territories may have been inadequately defined. Annual territories averaged $1,868 \pm 258 \text{ km}^2$. Annual territory sizes were correlated with pack size ($P = 0.034$). Some wolf packs (11% of 36 pack years) occasionally followed migratory caribou from 64 to 272 km when caribou and moose densities were rela-

tively low (i.e., $<200/1,000 \text{ km}^2$) within an individual territory. Recent colonization of northwest Alaska by moose may have altered wolf movement patterns.

2. Annual dispersal rates averaged 16%, but more wolves dispersed during 1990–91 and 1991–92 following a rabies epizootic than during other years. We could detect no difference in sex ratios between dispersing and nondispersing wolves. Wolves dispersed an average distance of $143 \pm 22 \text{ km}$. We could not detect differences in survival rates between dispersing and non-dispersing wolves. However, no dispersing wolves were known to have died from rabies.
3. Wolf densities within northwest Alaska were relatively low ($1.5\text{--}6.6 \text{ wolves}/1,000 \text{ km}^2$) in relation to available ungulate biomass indices, which should support wolf densities of $8.2\text{--}16.4/1,000 \text{ km}^2$. However, caribou were only seasonally available to most wolves. Annual finite rates of increase ranged from 0.64 to 1.43. Wolf densities increased during 1987 through spring 1990 and then declined in response to a combination of human harvest and an outbreak of rabies.
4. Annual survival during 1990–91 (0.457) and 1991–92 (0.482) was lower than annual survival during the remainder of the study (range = 0.585–0.654) and was attributed to a combination of high human harvests and a rabies epidemic.
5. 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 those mortalities. Sixty-four percent of the rabies-caused mortalities occurred during May and June. This study was the first to document that rabies could be a significant limiting factor of wolf populations.

6. Patterns of annual harvest according to harvest records were quite similar to that observed based upon radio-collared wolves. The numbers of wolves killed annually in northwest Alaska by local hunters and trappers is largely unknown because of poor compliance with state reporting and sealing regulations. Small (≤ 6) and large wolf packs responded similarly to overwinter mortality but small packs had greater rates of increase than large packs for a specific rate of mortality.
7. Nineteen wolf packs were observed on 168 carcasses 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. Wolves appeared to prey on calf and adult moose in proportion to their occurrence in the moose population, whereas adult caribou were killed disproportionately. Wolves did not select caribou calves.
8. Several wolf packs were relocated daily during March and April 1988 through 1990 to determine species composition of prey and kill rates. Thirteen wolf packs were observed on 68 carcasses of which 7 were scavenged. Packs of 1–4 individuals were responsible for all observed scavenging. Adult moose and caribou composed 41 and 36% of the observed kills, respectively. Calf moose were the third most common prey. Several instances of multiple kills of caribou were observed. Numbers of ungulates killed per successful wolf attack averaged 1.2 ($n = 54$). Kill rates averaged 4.6 ungulates/wolf/100 days. Carcass consumption averaged 53% at first observation 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 per day or 0.12 kg/kg wolf/day. Wolves stayed close to carcasses of adult female moose, adult bull moose, and adult male caribou an average of 2.0, 1.8, and 1.7 days, respectively. We failed to detect a correlation between pack size and number of ungulates killed/wolf/day or prey weight/wolf/day. Time interval between kills was negatively correlated with pack size ($r_s = -0.58$, $P = 0.04$). Comparisons among several studies in North America where caribou and moose were the principal prey species indicated that pack size and number of ungulates killed/wolf/day were not correlated, but pack size and available prey/wolf/day was negatively correlated. There is considerable variation within and among studies, and pack size is probably not a reliable indicator of kill rate.
9. Wolves preyed primarily on caribou when they were available. When caribou densities were low ($<200/1,000 \text{ km}^2$) wolves switched to moose. Adult caribou killed by wolves had femur marrow fat levels averaging 79%, whereas femur marrow fat levels in adult moose averaged 64%. We concluded that wolves preyed on caribou that had relatively high marrow fat values and may have been in good condition at time of death. However, moose preyed upon by wolves often were in marginal condition.
10. Based on estimated wolf densities within the range of the WACH, estimated kill rates determined during this study, and available ungulate population estimates, we estimated that wolves kill 6–7% of the caribou and 11–14% of the moose population annually. When caribou are present on a year-round basis they may dilute the effects of wolf predation on moose, which may allow the moose population to attain higher densities than would be expected. However, when caribou are absent, wolf predation may have a relatively higher impact on moose and cause the moose population to decline. Wolf densities could be higher in northwest Alaska if maintenance of current moose population

density were not a management priority.

LITERATURE CITED

- ADAMS, L. G., B. W. DALE, AND L. D. MECH. 1995. Wolf predation on caribou calves in Denali National Park, Alaska. Pages 245–260 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Can. Circumpolar Inst., Univ. Alberta, Edmonton.
- , AND R. O. STEPHENSON. 1986. Wolf survey, Gates of the Arctic National Park and Preserve—1986. U.S. Natl. Park Serv. Rep. NRSIR AR-86/04. 14pp.
- ALASKA DEPARTMENT OF FISH AND GAME. 1984. Western Arctic Caribou Herd strategic management plan. Alas. Dep. Fish and Game, Nome. 15pp.
- AMERICAN SOCIETY OF MAMMALOGISTS. 1987. Acceptable field methods in mammalogy: preliminary guidelines approved by the American Society of Mammalogists. J. Mammal. 65 (4, Suppl.) 18pp.
- BAKER, M. F., AND F. X. LEUTH. 1966. Mandibular cavity tissue as a possible indicator of condition of deer. Proc. Southeast. Assoc. Game and Fish Comm. 20:69–74.
- BALLARD, W. B. 1992. Bear predation on moose: a review of recent North American studies and their management implications. Alces Suppl. 1: 162–176.
- , L. A. AYRES, D. J. REED, S. G. FANCY, AND K. E. RONEY. 1993. Demography of grizzly bears in relation to hunting and mining development in northwest Alaska. U.S. Natl. Park Serv. Sci. Monogr. NPS/NRARO/NRSM-93/23. 112pp.
- , —, K. E. RONEY, AND T. H. SPRAKER. 1991. Immobilization of free-ranging gray wolves with a mixture of tiletamine hydrochloride and zolazepam hydrochloride. J. Wildl. Manage. 55:71–74.
- , R. FARRELL, AND R. O. STEPHENSON. 1983. Long distance movement by gray wolves (*Canis lupus*). Can. Field-Nat. 97:333.
- , A. W. FRANZMANN, AND C. L. GARDNER. 1982. Comparison and assessment of drugs used to immobilize Alaskan gray wolves (*Canis lupus*) and wolverine (*Gulo gulo*) from a helicopter. J. Wildl. Dis. 18:339–342.
- , C. L. GARDNER, J. H. WESTLAND, AND S. M. MILLER. 1981a. Use of mandible versus longbone to evaluate percent marrow fat in moose and caribou. Alces 17:147–164.
- , AND D. LARSEN. 1987. Implications of predator-prey relationships to moose management. Swed. Wildl. Res. Suppl. 1:581–602.
- , T. H. SPRAKER, AND K. P. TAYLOR. 1981b. Causes of neonatal moose calf mortality in south-central Alaska. J. Wildl. Manage. 45:335–342.
- , J. S. WHITMAN, AND C. L. GARDNER. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. 98. 54pp.
- BARICELLO, N., J. CAREY, R. SUMANIK, R. D. HAYES, AND A. M. BAER. 1989. The effects of wolf predation on Dall sheep in the northern Richardson Mountains. Yukon Fish and Wildl. Branch Rep., Whitehorse. 24pp.
- BERG, W. E., AND D. W. KUEHN. 1982. Ecology of wolves in northcentral Minnesota. Pages 4–11 in F. H. Harrington and P. C. Paquet, eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publ., Park Ridge, N.J.
- BERGERUD, A. T. 1974. Decline of caribou in North America following settlement. J. Wildl. Manage. 38:757–770.
- . 1983. The natural population control of caribou. Pages 14–61 in F. L. Bunnell, D. S. Eastman, and J. M. Peek, eds. Symposium on natural regulation of wildlife populations. For. Wildl. and Range Exp. Stn., Univ. Idaho, Moscow.
- . 1992. Rariness as an antipredator strategy to reduce predation risk for moose and caribou. Pages 1008–1021 in D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: populations. Elsevier Science Publ., Ltd., Essex, U.K.
- , AND W. B. BALLARD. 1988. Wolf predation on caribou: the Nelchina Herd case history, a different interpretation. J. Wildl. Manage. 52:344–357.
- , AND —. 1989. Wolf predation on Nelchina caribou: a reply. J. Wildl. Manage. 53:251–259.
- , AND J. P. ELLIOT. 1986. Dynamics of caribou and wolves in northern British Columbia. Can. J. Zool. 64:1515–1529.
- , AND F. MANUEL. 1969. Aerial census of moose in central Newfoundland. J. Wildl. Manage. 33:910–916.
- , AND R. E. PAGE. 1987. Displacement and dispersion of parturient caribou at calving as an antipredator tactic. Can. J. Zool. 65:1598–1606.
- BJORGE, R. R., AND J. R. GUNSON. 1983. Wolf predation of cattle on the Simonette River pastures in northwestern Alberta. Page 106–111 in L. N. Carbyn, ed. Wolves in Canada and Alaska: their status, biology, and management. Can. Wildl. Serv. Ser. 45., Ottawa.
- BOER, A. H. 1992. Fecundity of North American moose (*Alces alces*): a review. Alces Suppl 1:1–10.
- BURKHOLDER, B. L. 1959. Movements and behavior of a wolf pack in Alaska. J. Wildl. Manage. 23:1–11.
- CARBYN, L. N. 1974. Wolf predation and behavioral interactions with elk and other ungulates in an area of high prey diversity. Ph.D. Thesis, Univ. Toronto, Ont., Can. 233pp.
- . 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. J. Wildl. Manage. 47:963–976.
- CAUGHLEY, G. 1970. Eruption of ungulate popula-

- tions, with emphasis on Himalayan thar in New Zealand. *Ecology* 51:54–72.
- . 1978. Analysis of vertebrate populations. John Wiley and Sons, New York, N.Y. 234pp.
- CHEATUM, E. L. 1949. Bone marrow as an index of malnutrition in deer. *N.Y. State Conserv.* 3(5): 19–22.
- CONOVER, W. J. 1971. Practical nonparametric statistics. John Wiley and Sons, New York, N.Y. 462pp.
- DALE, B. W., L. G. ADAMS, AND R. T. BOWYER. 1995. Winter wolf predation in a multiple prey system, Gates of the Arctic National Park, Alaska. Pages 223–230 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Can. Circumpolar Inst., Univ. Alberta, Edmonton.
- DAU, J. 1989a. Wolf survey-inventory report 1987–1988, Game Management Unit 23. Pages 127–131 in S. O. Morgan, ed. Annual report of survey-inventory activities. Wolf. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-23-1, Job 14.0.
- . 1989b. Wolf survey-inventory report 1989–1991, Game Management Unit 23. Pages 127–131 in S. M. Abbott, ed. Annual report of survey-inventory activities. Wolf. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-23-3 and W-23-41, Job 14.0.
- DAVIS, J. L., AND P. VALKENBURG. 1978. Western Arctic Caribou Herd studies. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-17-8 and W-17-9. 43pp.
- , AND —. 1981. Natural mortality of Western Arctic Caribou. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-21-1. 19pp.
- , AND —. 1985. Qualitative and quantitative aspects of natural mortality of the Western Arctic Caribou Herd. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Final Prog. Rep., Proj. W-17-11, W-21-2, W-22-1, W-22-2, and W-22-3. 71pp.
- , —, AND D. J. REED. 1987. Correlations and depletion patterns of marrow fat in caribou bones. *J. Wildl. Manage.* 51:365–371.
- , —, AND H. V. REYNOLDS. 1980. Population dynamics of Alaska's Western Arctic Caribou Herd. Pages 595–604 in E. Reimers, E. Gaare, and S. Skjenneberg, eds. Proc. second international reindeer/caribou symp., Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk.
- DOERR, J. 1979. Population analysis and modeling of the Western Arctic Caribou Herd with comparisons to the other Alaskan *Rangifer* populations. M.S. Thesis, Univ. Alaska, Fairbanks. 340pp.
- EIDE, S., AND W. B. BALLARD. 1982. Apparent case of surplus killing of caribou by gray wolves. *Can. Field-Nat.* 96:87–88.
- FANCY, S. G., AND K. R. WHITTEN. 1991. Selection of calving sites by Porcupine Herd caribou. *Can. J. Zool.* 69:1736–1743.
- FRANZMANN, A. W., AND P. D. ARNESON. 1976. Marrow fat in Alaskan moose femurs in relation to mortality factors. *J. Wildl. Manage.* 40:336–339.
- , R. E. LERESHE, R. A. RAUSCH, AND J. L. OLDEMEYER. 1978. Alaskan moose measurements and weights and measurement-weight relationships. *Can. J. Zool.* 56:298–306.
- , C. C. SCHWARTZ, AND R. O. PETERSON. 1980. Causes of summer calf mortality on the Kenai Peninsula. *J. Wildl. Manage.* 44:764–768.
- FRIITTS, S. H. 1983. Record dispersal by a wolf from Minnesota. *J. Mammal.* 64:166–167.
- , AND L. D. MECH. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildl. Monogr.* 80. 79pp.
- FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildl. Monogr.* 105. 41pp.
- , AND L. B. KEITH. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *J. Wildl. Manage.* 44:583–602.
- , AND W. J. SNOW. 1988. Estimating wolf densities from radiotelemetry data. *Wildl. Soc. Bull.* 16:367–370.
- GASAWAY, W. C., R. D. BOERTJE, D. V. GRANGAARD, D. G. KELLYHOUSE, R. O. STEPHENSON, AND D. G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl. Monogr.* 120. 59pp.
- , R. O. STEPHENSON, J. L. DAVIS, P. E. K. SHEPHERD, AND O. E. BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildl. Monogr.* 84. 50pp.
- HABER, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. Thesis, Univ. British Columbia, Vancouver, Can. 817pp.
- HAKALA, J. B. 1954. Predator control activities. Alas. Native Serv., Kotzebue. 3pp.
- HARRINGTON, F. H., P. C. PAQUET, J. RYON, AND J. C. FENTRESS. 1982. Monogamy in wolves: a review of the evidence. Pages 209–222 in F. H. Harrington and P. C. Paquet, eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publ., Park Ridge, N.J.
- HAYES, R. D., A. M. BAYER, AND D. G. LARSON. 1991. Population dynamics and prey relationships of an exploited and recovering wolf population in the southern Yukon. Yukon Fish and Wildl. Branch Final Rep. TR-91-1. 67pp.
- HEISEY, D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.* 49:668–674.
- JAMES, D. 1983. Seasonal movements, food habits, and predation rates of wolves in northwest Alaska. M.S. Thesis, Univ. Alaska, Fairbanks. 105pp.
- . 1984. Home range dynamics of wolf packs on winter range of the Western Arctic Caribou

- Herd. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Final Rep., Proj. W-22-2, 5pp.
- KELLY, M. W. 1954. Observations afield on Alaskan wolves. Proc. Alas. Sci. Conf. 5:1-8.
- KOLENOSKY, G. B. 1972. Wolf predation on wintering deer in eastcentral Ontario. J. Wildl. Manage. 36:357-369.
- KUYT, E. 1972. Food habits of wolves on barren-ground caribou range. Can. Wildl. Serv. Rep. Ser. 21. 36pp.
- LARSEN, D. N., AND D. D. JAMES. 1987. Wolf survey-inventory report 1985-1986, Game Management Unit 23. Pages 45-47 in B. Townsend, ed. Annual report of survey-inventory activities. Wolf. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-22-5, Job 14.0.
- , AND —. 1988. Wolf survey-inventory report 1986-1987, Game Management Unit 23. Pages 51-53 in S. O. Morgan, ed. Annual report of survey-inventory activities. Wolf. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-22-6, Job 14.0.
- , M. A. SPINDLER, AND D. D. JAMES. 1986. Moose population estimate, trend, and distribution survey on Selawik National Wildlife Refuge, Game Management Unit 23, 1985. Selawik Natl. Wildl. Refuge Prog. Rep. 86:1. 15pp.
- MACHIDA, S. 1992. Caribou survey-inventory progress report 1989-91, Game Management Units 21D, 22A, 22B, 23, 24, and 26A. Pages 132-150 in S. M. Abbot, ed. Survey-inventory management report. Caribou. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-23-3 and W-23-4, Study 3.0.
- MECH, L. D. 1977. Population trend and winter deer consumption in a Minnesota wolf pack. Pages 55-83 in R. L. Phillips and C. Jonkel, eds. Proc. 1975 Predator Symp. Bull., Montana For. Conserv. Exp. Stn., Univ. Montana, Missoula.
- , AND G. D. DELGIUDICE. 1985. Limitations of the marrow fat technique as an indicator of body condition. Wildl. Soc. Bull. 13:204-206.
- , T. J. MEIER, J. W. BURCH, AND L. G. ADAMS. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. Pages 231-249 in L. N. Carbyn, S. H. Fritts, and D. R. Siep, eds. Ecology and conservation of wolves in a changing world. Can. Circumpolar Inst. Univ. Alberta, Edmonton.
- MESSIER, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. Can. J. Zool. 63:1068-1077.
- . 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478-488.
- , AND M. CRÈTE. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia (Berlin) 65:503-512.
- MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Mid. Nat. 37:223-249.
- MURIE, A. 1944. The wolves of Mount McKinley. U.S. Natl. Park Serv. Fauna Ser. 5. 238pp.
- NEILAND, K. A. 1970. Weight of dried marrow as an indicator of fat in caribou femurs. J. Wildl. Manage. 34:904-907.
- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1989. Applied linear regression models. IRWIN, Homewood, Ill. 500pp.
- NOWAK, R. M. 1983. A perspective on the taxonomy of wolves in North America. Pages 10-19 in L. N. Carbyn, ed. Wolves in Canada and Alaska: their status, biology, and management. Can. Wildl. Serv. Rep. Ser. 45. 135pp.
- OOSENBURG, S. M., AND L. N. CARBYN. 1982. Winter predation on bison and activity patterns of a wolf pack in Wood Buffalo National Park. Pages 43-53 in F. H. Harrington and P. C. Paquet, eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publ., Park Ridge, N.J.
- OTT, L. 1988. An introduction to statistical methods and data analysis. PWS-Kent Publ. Co., Boston, Mass. 835pp.
- PACKARD, J. M., AND L. D. MECH. 1980. Population regulation in wolves. Pages 135-150 in M. N. Cohen, R. S. Malpass, and H. G. Klein, eds. Biosocial mechanisms of population regulation. Yale Univ. Press, New Haven, Conn.
- PARKER, G. R. 1972. Biology of the Kaminuriak population of barren-ground caribou. Part I. Can. Wildl. Serv. Rep. 20, Ottawa, Ont. 95pp.
- PETERSON, R. L. 1955. North American moose. Univ. Toronto Press, Ont., Can. 280pp.
- PETERSON, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Natl. Park Serv. Sci. Monogr. Ser. 11. 210pp.
- , AND R. E. PAGE. 1988. The rise and fall of Isle Royale wolves, 1975-1986. J. Mammal. 69: 89-99.
- , J. D. WOOLINGTON, AND T. N. BAILEY. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. 88. 52pp.
- PROMBERGER, C. 1991. Influence of scavengers on the consumption of wolves in the wild. Trans. Congr. Int. Union Game Biol. 20:396 (abstr. only).
- QUIMBY, R. L. 1982. Wolf survey-inventory progress report 1980-81, Game Management Unit 23. Pages 99-196 in R. A. Hinman, ed. Annual report of survey-inventory activities. Part IV. Fur-bearers, small game, walrus, and wolverine. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-19-1 and W-19-2.
- SEIP, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Can. J. Zool. 70:1494-1503.
- SERGEANT, D. E., AND D. H. PIMLOTT. 1959. Age determination in moose from sectioned incisor teeth. J. Wildl. Manage. 23:315-321.
- SKOGLAND, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. J. Anim. Ecol. 54:359-374.

- SKOOG, R. O. 1968. Ecology of caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. Thesis, Univ. California, Berkeley. 699pp.
- SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, Calif. 776pp.
- SPINDLER, M. A. 1989. Distribution and abundance of caribou on Selawik National Wildlife Refuge, Alaska 1984–1989. U.S. Fish and Wildl. Serv. Prog. Rep. SNWR 89-5. 61pp.
- _____. 1992. Wolf distribution, movements, abundance, and predation on the Koyukuk/Nowitna National Wildlife Refuge. U.S. Fish and Wildl. Serv., Koyukuk/Nowitna Natl. Wildl. Refuge Complex Prog. Rep. 92-4. 21pp.
- STEPHENSON, R. O. 1978. Characteristics of exploited wolf populations. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Final Rep., Proj. W-17-3 and W-17-8. 21pp.
- _____, W. B. BALLARD, C. A. SMITH, AND K. RICHARDSON. 1995. Wolf biology and management in Alaska 1981–91. Pages 43–54 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Can. Circumpolar Inst., Univ. Alberta, Edmonton.
- _____, AND D. JAMES. 1982. Wolf movements and food habits in northwest Alaska. Pages 26–42 in F. H. Harrington and P. C. Paquet, eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publ., Park Ridge, N.J.
- _____, AND L. J. JOHNSON. 1972. Wolf report. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-17-3. 51pp.
- _____, AND _____. 1973. Wolf report. Alas. Dep. Fish and Game, Fed. Aid in Wildl. Restor. Prog. Rep., Proj. W-17-4 and W-17-5. 52pp.
- SUMANIK, R. S. 1987. Wolf ecology in the Kluane Region, Yukon Territory. M.S. Thesis, Michigan Tech. Univ., Houghton. 102pp.
- U.S. DEPARTMENT OF INTERIOR. 1987. Selawik National Wildlife Refuge. Wilderness area planning: environmental impact statement. U.S. Gov. Printing Off., Washington, D.C. 230pp.
- VAN BALLEMBERGHE, V. 1985. Wolf predation on caribou: the Nelchina case history. *J. Wildl. Manage.* 49:711–720.
- _____. 1989. Wolf predation on the Nelchina Caribou Herd: a comment. *J. Wildl. Manage.* 53: 243–250.
- VAN CAMP, J., AND R. GLUCKIE. 1979. A record long-distance move by a wolf (*Canis lupus*). *J. Mammal.* 60:236–237.
- WHITTEN, K. R., G. W. GARNER, F. J. MAUER, AND R. B. HARRIS. 1992. Productivity and early calf survival in the Porcupine Caribou Herd. *J. Wildl. Manage.* 56:201–212.
- WILKINSON, L., M. HILL, J. P. WELNA, AND G. K. BIRKENBEVEL. 1992. SYSTAT for Windows: statistics, version 5 ed. SYSTAT, Inc., Evanston, Ill. 750pp.
- ZAR, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, N.J. 718pp.

Received 1 November 1994.

Accepted 31 July 1996.

APPENDIX

Summary of wolves captured and radio collared during April 1987 through April 1991 in northwest Alaska.

ID no.	Pack ^a	Date immobilized	Sex	Age	Weight (kg)	Status as of 15 Jul 92	Fate on date of last contact
1	1	15 Apr 87	M	Adult	43.1	Dead	Shot 27 Feb 88 (snowmobile).
2	2	15 Apr 87	F	Yearling	44.0	Missing	29 Jul 89.
		14 Apr 89		Adult	45.4		
3	2	15 Apr 87	M	Adult	49.9	Dead	Starvation—16 Dec 90–2 Mar 91.
4	2	15 Apr 87	F	Pup	34.0	Dead	Dispersed 16 km to Huslia 24 Jun 88–21 Sep 88; killed by wolves 28 Sep 89.
		7	14 Apr 89		39.9		
5	3	16 Apr 87	F	Pup		Dead	Shot 8 Jan 88 (snowmobile).
6	3	16 Apr 87	M	Adult		Dead	Dispersed 328 km to Wulik R. 7 Jul–Nov 87; shot Nov 87 (snowmobile).
7	4	16 Apr 87	F	Adult	40.8	Dead	Shot 2 Apr 90 (snowmobile).
		24 Apr 88		Adult	37.6		
		10 Apr 89		Adult	39.0		
8	4	16 Apr 87	M	Adult	50.8	Dead	Shot Jan 88 (snowmobile).
9	5	17 Apr 87	M	Adult	55.3	Dead	Dispersed 375 km to Ray Mts. 24 Nov–17 Dec 87; shot 21 Feb 89 (aircraft).
10	5	17 Apr 87	F	Pup		Dead	Shot Mar 91 (snowmobile).
		26 Apr 88		Yearling	47.6		
		10 Apr 89		Adult			
11	1	17 Apr 87	M	Adult		Dead	7 Jun 89 natural death—old age.
12	2	23 Mar 88	F	Pup	35.4	Missing	After 19 Jul 89.
		11 Jun 88		Yearling	33.1		
13	6	23 Apr 88	M	Yearling	43.1	Dead	Moved 167 km to Shaktoolik R. and returned; shot Mar 89 (snowmobile).
		13 Nov 88		Adult	42.6		
14	1	24 Apr 88	F	Adult	44.9	Dead	Shot Jan–Mar 89 (aircraft).
15	6	24 Apr 88	M	Adult	46.3	Dead	Moved 167 km to Shaktoolik R. and returned; shot 9 Mar 89 (snowmobile).
16	6	24 Apr 88	F	Pup	28.6	Dead	Shot 3 Mar 91 (snowmobile).
		15 May 90		Adult	36.3		
17	6	24 Apr 88	F	Pup	31.8	Dead	Dispersed 77 km to Kateel R. 22 Feb–4 Apr 89; moved 64 km to Shaktoolik R. and returned 6 Nov 89–Dec 89; shot Dec 89 (snowmobile).
18	5	26 Apr 88	M	Pup	49.0	Missing	Dispersed 64 km to Kelly R.; missing after Jul 89.
19	5	26 Apr 88	M	Pup	47.2	Dead	Rabies probable; 29 May 90.
		10 Apr 89		Yearling	50.8		
20	5	26 Apr 88	M	Yearling	49.9	Dead	Sacrificed 27 Apr 88.
		27 Apr 88		Yearling			
21	5	26 Apr 88	M	Yearling	47.2	Dead or dropped collar	Dispersed 64 km to Waring Mts. 3 Jun–17 Aug 88. Dead or dropped collar by 28 Aug 91.
11	9 Apr 91			Adult			
22	12	3 Aug 88	F	Pup	11.3	Dead	Shot 5 Dec 88 (snowmobile).
		12 Nov 88		Pup	24.9		
23	1	14 Nov 88	F	Pup		Dead	Shot 4 Jan 89 (snowmobile).
24	3	27 Jun 88	M	Adult	47.6	Dead	Shot 18 Feb 89 (snowmobile).
		14 Nov 88		Adult	49.9		
25	1	14 Nov 88	M	Pup	34.0	Dead	Moved 264 km to Shaktoolik R. and returned 14 Nov 88–10 Mar 89; shot 10 Mar 89 (snowmobile).
26	4	15 Nov 88	M	Adult	46.3	Dead	Shot 15 Jan–11 Mar 89 (snowmobile).
27	12	15 Nov 88	M	Adult	44.5	Missing	Dispersed 16 km west; missing after 1 May 90.
28	12	15 Nov 88	M	Pup	31.8	Dead	Shot 3 Dec 88 (snowmobile).
29	1	9 Apr 89	F	Pup	42.6	Dead	Shot 1 May 89 (snowmobile).
30	1	9 Apr 89	F	Pup	37.2	Dead	Rabies confirmed; 19 Oct 89–14 Feb 90.

Appendix. Continued.

ID no.	Pack ^a	Date immobilized	Sex	Age	Weight (kg)	Status as of 15 Jul 92	Fate on date of last contact
31	13	9 Apr 89	F	Yearling	38.6	Dead	Rabies probable; 26 Jul 89–21 Aug 89.
32	13	9 Apr 89	F	Pup	38.1	Dead	Rabies probable; 1 May 90–20 Jun 90.
		17 Apr 90		Yearling	36.7		
33	11	10 Apr 89	F	Adult	47.2	Dead	Dispersed 106 km west between 18 Apr–28 Aug 90.
		14 Apr 90		Adult	39.9		Shot Mar 92 (assumed date) ^b .
34	5	10 Apr 88	F	Adult	47.6	Dead	Shot 23 Jan 92 (snowmobile).
35	5	10 Apr 89	F	Pup		Missing	Dispersed 166 km to Round Mt. on 2 Apr 90; missing after 7 Apr 90.
36	3	13 Apr 89	F	Pup	38.1	Missing	Dispersed 272 km to Shaktoolik R. 12 Oct 90–11 Mar 91; missing after 11 Mar 91.
37	3	13 Apr 89	F	Adult	44.9	Missing	Missing after 25 May 89.
38	3	13 Apr 89	M	Pup	45.8	Dead	Dispersed 148 km northwest to Natmotirak Creek 25 May–6 Sep 89; shot 12 Jan 90 (snowmobile).
39	3	13 Apr 89	F	Pup		Missing	Missing after 6 Apr 90.
40	6	14 Apr 89	F	Pup	34.5	Missing	Missing after 25 Mar 90.
41	7	14 Apr 89	M	Adult	49.0	Dead	Shot Feb 91.
42	2	14 Apr 89	F	Pup	34.5	Dead	Starvation 2–31 Mar 91.
43	2	14 Apr 89	M	Pup	40.8	Dead	Shot Mar 91 (snowmobile).
44	2	14 Apr 89	M	Adult	49.0	Missing	Missing after 1 May 89.
45	8	15 Apr 89	F	Adult	36.3	Missing	Missing after 28 Sep 89.
46	9	15 Apr 89	F	Pup	39.0	Alive	Dispersed 113 km to Purcell Mt. 8 Oct 91.
		15 Apr 90		Yearling	44.5		9 Oct 91.
47	9	15 Apr 89	F	Adult	39.9	Alive	Missing between 16 Apr–20 Jun 89.
48	10	15 Apr 90	M	Adult	51.7	Missing	Moved 85 km to Kobuk R. 28 Oct 89–14 Feb 90; shot 14 Feb–23 Mar 90 (snowmobile).
49	14	19 Apr 89	M	Adult	42.6	Dead	Missing after 1 Aug 90.
50	13	12 Apr 90	M	Adult	40.4	Missing	Shot Feb 91 (snowmobile).
51	7	12 Apr 90	F	Pup	44.5	Dead	Rabies confirmed; 1 May 90.
52	5	13 Apr 90	F	Pup	38.1	Dead	Rabies probable 3 Jun 90–31 Jul 90.
53	5	13 Apr 90	F	Pup	43.1	Dead	Missing after 1 May 90.
54	5	13 Apr 90	M	Pup	43.5	Missing	Rabies probable; 29 May 90.
55	5	13 Apr 90	F	Yearling	46.7	Dead	Rabies confirmed; 1 May 90.
56	5	13 Apr 90	F	Pup	37.2	Dead	Dispersed minimum of 154 km to Upper Tag R. 21 Jun–12 Oct 90; missing after 12 Oct 90.
57	15	13 May 90	F	Adult	50.3	Missing	Suspect shot 5 Dec 90–2 Mar 91.
58	15	13 Apr 90	F	Pup	39.5	Dead	Dispersed 64 km northeast to Noatoak R. 1 May 90–14 May 91; alive 15 Jul 92.
59	15	13 Apr 90	M	Adult	47.6	Alive	Shot 8 Dec 90–3 Jan 91 (snowmobile).
60	15	13 Apr 90	M	Yearling	44.9	Dead	After 1 Apr 91 suspect shot with 9 pack members (snowmobile).
61	15	13 Apr 90	F	Yearling	40.8	Probable dead	Missing after 10 May 91.
62	2	14 Apr 90	M	Pup	37.2	Missing	Starvation 2–31 Mar 91.
63	2	14 Apr 90	F	Pup	39.0	Dead	Missing after 28 Aug 91.
64	2	14 Apr 90	F	Adult	39.9	Missing	Moved 272 km to Shaktoolik R. and returned to Dunes area (135 km northwest of territory) 12 Oct 90–14 Apr 91; missing after 9 Oct 91.
65	3	14 Apr 90	M	Pup	41.7	Missing	Moved 272 km to Shaktoolik R. and returned to territory 12 Oct 90–15 May 91; dispersed 77 km to Dunes area 14 May–28 Aug 91; alive 13 Jul 92.
66	3	14 Apr 90	M	Yearling	41.7	Alive	

Appendix. Continued.

ID no.	Pack ^a	Date immobilized	Sex	Age	Weight (kg)	Status as of 15 Jul 92	Fate on date of last contact
67	3	14 Apr 90	F	Yearling	39.0	Dead	Rabies probable; 21–28 Jun 90.
68	11	14 Apr 90	M	Adult	47.2	Dead	Dispersed 270 km to Shaktoolik R. 20 Jul 90–11 Mar 91; shot 21 Mar 91 (snowmobile).
69	11	14 Apr 90	M	Yearling	45.4	Missing	Dispersed 166 km to Tagagawick R. 5 Dec 90–3 Mar 91; missing after 3 Mar 91.
70	16	18 Apr 90	M	Adult		Dead	Rabies confirmed; 1 Aug–12 Oct 90.
71	9	15 Apr 90	M	Adult	54.4	Alive	9 Oct 91.
72	9	15 Apr 90	F	Yearling	39.0	Missing	Missing after 21 Jun 90.
73	9	15 Apr 90	M	Adult	48.1	Dead	Shot 11 Mar–9 Apr 91 (snowmobile).
74	6	15 Apr 90	M	Adult	49.4	Missing	Missing after 24 Jul 90.
75	6	15 Apr 90	M	Pup	41.7	Missing	Missing after 12 Oct 90.
76	16	18 Apr 90	F	Yearling		Dead	Shot 2–3 Mar 91 (snowmobile).
77	5	7 Apr 91	F	Adult	43.1	Dead	Shot Mar 92 (assumed date) ^b (snowmobile).
78	17	7 Apr 91	M	Adult	44.5	Alive	15 Jul 92.
79	17	7 Apr 91	F	Adult	40.8	Alive	Dispersed 72 km to L. Kobuk Sand Dunes with pups 28 Aug–9 Oct 91; alive 15 Jul 92.
80	2	8 Apr 91	F	Adult	46.7	Dead	Shot Mar 92 (assumed date) ^b (snowmobile).
81	2	8 Apr 91	M	Adult		Dead or dropped collar	2 Jul 91.
82	18	9 Apr 91	M	Yearling	46.3	Alive	Dispersed 142 km to Selawik Hills 9 Apr–10 May 91; alive 9 Oct 91.
83	18	9 Apr 91	F	Adult		Dead	Cause unknown, rabies possible; 29 Apr–19 Jun 91.
84	5	9 Apr 91	M	Yearling	44.5	Alive	13 Jul 92.
85	19	9 Apr 91	M	Pup	49.0	Dead	Shot Mar 92 (assumed date) ^b (snowmobile).
86	19	9 Apr 91	M	Pup	49.9	Dead	Dispersed 154 km to mouth Kukpowruk R. 8 Oct–15 Dec 91; shto 15 Dec 91 (snowmobile).

^a Pack names: 1 = Rabbit Mt., 2 = Purcell Mt., 3 = Pick River, 4 = Jade Mt., 5 = Nuna Creek, 6 = Inguruksukruk, 7 = Huslia, 8 = Lower Tagagawick, 9 = Upper Tagagawick, 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.