

Winter Wolf Predation in a Multiple Ungulate Prey System, Gates of the Arctic National Park, Alaska

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We investigated patterns of winter wolf predation, including prey selection, prey switching, kill rates, carcass utilization, and consumption rates for four wolf packs during three different study periods (March 1989, March 1990, and November 1990) in Gates of the Arctic National Park and Preserve, Alaska. Wolves killed predominately caribou (165 caribou, seven moose, and five Dall sheep) even when moose and sheep were more abundant. Prey selection varied between study periods. More moose were killed in March 1989, a particularly deep snow year, and more sheep were killed in November 1990 than during other periods. Overall kill rates ranged from 0–8 days/ungulate killed ($\bar{x} = 2.0$, $SD = 1.6$) and did not vary between study periods. Pack size and species killed explained significant variation in the length of time intervals between kills. Although caribou density varied nearly 40-fold between pack territories, it had little influence on predation characteristics except at low densities, when kill rates may have declined. Caribou distribution had marked effects on wolf predation rate.

Introduction

Caribou (*Rangifer tarandus*) are an important food resource for wolves (*Canis lupus*) throughout much of their sympatric range (Murie 1944, Banfield 1954, Kelsall 1960, Kuyt 1972, Bergerud 1978a, 1983, Gauthier and Theberge 1986), and wolves are thought to have a major influence on the dynamics of caribou populations (Kuyt 1972, Miller and Broughton 1974, Bergerud 1974a, 1980, Davis et al. 1980). Despite this close association, fundamental knowledge of wolf-caribou relationships is lacking, and much must be inferred from studies of wolves and other ungulate prey, such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*). Unlike other ungulate prey, barren-ground caribou are a unique resource for wolves because they are migratory, highly mobile, may occur in large groups, and their abundance and distribution may vary widely (Bergerud 1974b, Cumming 1975, Stephenson and James 1982, Valkenburg et al. 1983). Information inferred from studies of more sedentary prey may not be applicable to wolf-caribou relationships. Further, because wolves must respond behaviorally to dramatic changes in caribou availability, local abundance of caribou will affect utilization of other available ungulate prey such as Dall sheep (*Ovis dalli dalli*) and moose. In multiple prey systems, factors governing prey selection and the rate at which wolves kill various prey are largely unknown.

As part of a study of wolf ecology and demography in Gates of the Arctic National Park and Preserve, we deter-

mined prey selection and kill rates in early and late winter. We predicted that deep snow conditions in late winter would result in higher kill rates due to increased vulnerability of caribou, and that wolves would switch to other ungulate prey when caribou are scarce.

We evaluated the influence of caribou abundance, snow depth, and season on wolf prey selection and kill rates. Winter 1988–1989 witnessed a near record snowfall, whereas winter 1989–1990 was near average. Therefore, characteristics of predation during March 1989 and March 1990 should reflect differences caused by variation in late-winter snow depth. The November 1990 study period represents much shallower, early-winter snow depths. Variation in predation characteristics among the November and March study periods may be due to seasonal variation in prey condition and snow depth.

Study Area

Gates of the Arctic National Park straddles the central Brooks Range in northern Alaska (68° N 153° W), and encompasses a roadless wilderness of approximately 30,000 km². The climate is largely arctic to the north of the continental divide and subarctic to the south (NPS 1987). The entire region is characterized by long, cold winters and short, warm summers. Yearly precipitation commonly ranges from 130 to 450 mm, and yearly snowfall from 89 to 203 cm. Temperatures range from -34° C to 21° C (NPS 1987).

Cumulative snowfall in late March 1989 at Bettles Field (approximately 80 km east of the study area) was 240 cm, compared to the 40-year mean of 180 cm. Cumulative snowfall in late March 1990 was also above average (218 cm), however, 79 cm fell during March. Cumulative snowfall in late November 1990 was 91 cm. We assumed that snowfall and other characteristics were similar among pack territories.

The central Brooks Range is characterized by wide river valleys and steep rugged mountains. Boreal forest (taiga) predominates along the southern border of Gates of the Arctic National Park and extends northward up south-flowing drainages to the continental divide. Shrub thickets are common above treeline. Alpine tundra occurs at higher elevations and moist tundra communities occur in the foothills and along north-flowing drainages (NPS 1987).

Wolves are distributed throughout Gates of the Arctic National Park at approximately 7.4 wolves/1000 km² (Adams and Stephenson 1986), a density typical of northern wolf populations (Chapman and Feldhamer 1982). Wolves in the study area are nonmigratory. Of the four packs observed in this study, only one was harvested. The Iniakuk Pack (IP) was reduced by two to three wolves each year because of trapping, however, the alpha wolves survived throughout the study period.

In addition to wolves, predators of ungulates include lynx (*Lynx canadensis*), wolverines (*Gulo gulo*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*). Large prey for wolves consists of caribou, Dall sheep, and moose. Dall sheep and moose are locally abundant at about 0.5/km² on suitable range (Singer 1984a) and 0.12/km² (this study), respectively, whereas caribou are seasonally abundant. Although caribou are nearly always present, caribou use the area primarily during autumn and winter (Cameron and Whitten 1979). The Western Arctic Caribou Herd (WAH), estimated at 415,000 caribou in 1990 (P. Valkenburg, ADFG, pers. commun.) migrates southward and eastward toward the area in August–September, and a small number often winters there. WAH caribou do not show annual fidelity to winter ranges, but do not change ranges during any particular winter (Valkenburg et al. 1983). Small prey are diverse and include snowshoe hares (*Lepus americanus*) and beaver (*Castor canadensis*).

Methods

Prey Abundance and Distribution

Boundaries of wolf-pack territories were determined from observations obtained from April 1987 through March 1990, and delineated using the minimum convex polygon method (Mohr 1947). Relative abundance of moose and caribou in each pack territory was estimated during each 30-day period by aerial surveys (Gasaway et al. 1983). Relative moose densities were estimated by aerial surveys with corrections

for sightability (Gasaway et al. 1986). Survey units of approximately 30 km² were surveyed with a search intensity of about 0.5 minutes/km². The sightability correction factor was determined by counting six or seven units before randomly selecting one survey unit to be recounted at a higher survey intensity (2 minutes/km²). Density estimates for moose were calculated and statistically evaluated as described by Gasaway et al. (1986). These estimates of moose density may not be directly comparable to those from other studies because they: 1) include areas of unsuitable moose habitat; and 2) include late winter surveys (Gasaway et al. 1986).

The minimum number of caribou within each pack territory was also determined during the moose survey. It was impossible to develop a sightability correction factor because groups of caribou frequently crossed survey unit boundaries between standard and intensive surveys.

Dall sheep were not surveyed due to low sightability in winter. Although the winter distribution of sheep was not known, sheep movements from summer ranges were probably not extensive relative to wolf pack territory size (Ayres 1986). Summer sheep densities were previously estimated at about 0.5 sheep/km² on suitable ranges (Singer 1984a, Adams 1988).

Predation Characteristics

Prey selection, kill rate, and carcass utilization were estimated during 30-day study periods in March 1989, March 1990, and November 1990. Study packs were chosen because their territories had similar vegetation, topography, and excellent snow characteristics for tracking. Four packs with radio-collared members were located daily during each 30-day period, except for one day in March 1990, and one day in November 1990 when weather conditions prevented flying. All packs were relocated once or twice daily with Piper (PA-18) aircraft equipped with telemetry-receiving equipment (Carbyn 1983b). Upon visually locating wolves, the pelage color, number, and activity of individual wolves were recorded. The immediate area was searched for additional wolves or the presence of kills. Local vegetation, topography, and snow conditions were recorded. Whenever possible packs were backtracked to the previous location to find kills and additional pack members that would otherwise be missed.

The species and number of ungulate kills were determined from the air based on hair color, carcass size, presence of antlers or horns, and tracks at the kill site. The proportion of the carcass that had been consumed was visually estimated. All movements, activities, and kill locations were recorded on 1:63,360 or 1:250,000 scale topographic maps.

Ground investigation of 110 of 177 total kills was made three to 14 days after wolves abandoned the carcasses. At kill sites we verified species of the kill, and where sufficient evidence remained, we identified or collected specimens

Table 1. Relative moose and caribou density estimates and wolf numbers for selected wolf packs in Gates of the Arctic National Park and Preserve, Alaska.

<i>Study Period</i>	<i>Pack</i>	<i>Caribou/km²</i>	<i>Moose/km²</i>	<i>Wolves</i>
March 1989	Walker L.	2.34	0.12	7
	Iniakuk	0.31	0.09	5
	Unakserak	0.08	0.11	12
	Sixty Mile	0.07	0.12	11
March 1990	Walker L.	1.19	0.14	10
	Iniakuk	0.19	0.12	5
	Unakserak	0.21	0.09	8
	Pingaluk	0.50	0.08	7
November 1990	Walker L.	NA	NA	15
	Iniakuk	0.06	0.24	10 ¹
	Unakserak	0.41	0.12	13
	Pingaluk	0.24	0.13	11

NA = No prey surveys were conducted.

¹ Three pups are harvested early in the rate estimation period reducing pack size to 7 wolves.

(e.g., teeth, mandibles, pelvises) to determine the sex and age classes of the ungulate.

A single kill rate for each pack was estimated during each 30-day study period. Rates were estimated for a period beginning the day after location of a fresh kill and ending on the day the last kill was located. Periods of rate estimation ranged from 11–27 days. Kill rates were expressed as kills/wolf/day when assessing effects on prey populations. Wolf groups were quantitatively described as travelling pack size (Messier 1985a), because pack members are not always found together due to temporary or permanent dispersal, mortality, or fragmentation into subgroups for hunting. This measure constitutes the mean number of wolves seen in each pack during the study period. Lengths of intervals between kills (days/kill/pack) were used to analyze factors influencing kill rate.

Statistical Analyses

Analysis of covariance was used to determine differences in the mean interval between kills for different seasons and snow depths using travelling pack size, caribou density, and the numbers and species of previous kills as covariates. This statistical model was used to evaluate variation in interval length due to main effects (i.e., snow, season) while controlling for confounding variation of measurable covariates. By employing this method there was no need to adjust interval lengths for the size or number of prey killed (Ballard et al. 1987). Because of a slightly skewed distribution near zero, intervals were transformed by adding 0.5 to the interval and taking the square root of that sum (Steel and Torrie 1980).

Linear regression models were used to assess association between normal variables; log-linear models were used to assess differences in frequencies of observed behaviors; and logistic regression was employed to assess factors associated with the proportion of kills located by back-tracking wolves.

Results

Prey Availability and Prey Selection

Caribou density within pack territories ranged from 0.06–2.34 caribou/km², while moose density ranged from 0.08–0.24 moose/km² (Table 1). Wolves primarily killed caribou (93%) during the study (Table 2), but prey selection was not independent of study period (Chi square = 12.79, d.f. = 4, $P = 0.012$). The high numbers of moose killed in March 1989, and sheep in November 1990, constituted the major contribution to the Chi-square statistic.

There was no difference (Chi square < 0.001, d.f. = 1, $P = 0.98$) between March 1989 and March 1990 in the proportion of calves in known-age caribou kills, so prey selection for those two study periods was pooled. The resulting age composition of known-age caribou kills was dependent on season (Chi square = 4.94, d.f. = 1, $P = 0.0262$) with a higher proportion of calves killed in November 1990 (35%) than during March 1989 and March 1990 (13%).

Kill Rate Estimation

Wolves spent little time on carcasses as 39% of 177 kills were located by backtracking the wolves toward their location from the previous day. There was no relationship be-

Table 2. Prey selection and kill rates for wolves in Gates of the Arctic National Park, Alaska in March 1989, March 1990 and November 1990.

Pack	Travelling Pack size	Rate Est Period (Days)	Kills			Caribou/ Wolf/Day	kg/Wolf/ Day
			Caribou	Moose	Sheep		
<u>March 1989</u>							
Walker L.	6.1	27	17	3	0	0.10	12.0
Iniakuk	4.8	26	12	2	0	0.10	11.1
Unakserak	7.7	24	13	1	0	0.07	5.4
Pingaluk	2.0	19	2	0	0	0.05	3.6
Sixtymile	8.5	26	14	0	0	0.06	4.4
<u>March 1990</u>							
Walker L.	9.8	21	19	0	0	0.09	6.3
Iniakuk	4.4	22	10	0	0	0.10	7.1
Unakserak	6.0	19	12	0	1	0.11	7.6
Pingaluk	6.1	20	10	0	0	0.08	5.6
<u>November 1990</u>							
Walker L.	14.3	11	15	0	0	0.10	5.7
Iniakuk	5.4	16	9	0	0	0.10	6.3
Unakserak	12.2	19	25	0	1	0.11	6.7
Pingaluk	10.6	19	7	1	3	0.03	4.1

tween kill rate and the proportion of kills located by backtracking ($P = 0.95$, d.f. = 10, $n = 12$).

Kill Rates on Caribou and Caribou Availability

Rates at which wolves killed caribou ranged from 0.37–1.36 caribou/pack/day or 0.03–0.11 caribou/wolf/day. Overall, each wolf killed 0.09 ($SD = 0.02$, $n = 12$) caribou/day. Only at low caribou densities did caribou kill rate seem to be influenced by caribou abundance (Fig. 1). We excluded data from the Pingaluk pair of wolves for March 1989, when only two kills were documented during the rate estimation period. The Pingaluk pair killed an adult moose two days after the rate estimation period ended. Including this kill would result in doubling the daily available ungulate biomass for this pair.

Multiple Kills

Wolves frequently killed more than one animal during an attack on a group of caribou. Based on carcass locations and tracks, wolves killed 1.2 caribou per successful attack (range 1–4). The mean number of kills per successful attack was not correlated with travelling pack size ($r^2 = 0.06$, $P = 0.444$) or mean caribou group size within a pack territory ($r^2 = 0.02$, $P = 0.616$).

Effects of Snow Depth and Season on Kill Rate

Intervals between kills ranged from zero to eight days with a mean of two days ($SD = 1.6$, $n = 118$). Interval length did not vary significantly among packs (ANCOVA, $F = 0.25$, d.f. = 4, $P = 0.908$) when travelling pack size, caribou density, and food availability (number and species of ungulates killed at each successful attack) were held as covariates.

Packs were pooled to evaluate the effects of snow and season, because kill rates among packs were not significantly different. The snow-season factor had three levels, March 1989 (late winter near record snow), March 1990 (late winter above average snow), and November 1990 (early winter conditions). Kill rates during these periods were not significantly different (Fig. 2) (ANCOVA $F = 0.08$, d.f. = 2, $P = 0.923$). The regression of covariates explained significant ($F = 3.32$, d.f. = 3, $P = 0.023$) variation in interval lengths. Travelling pack size and food availability were significant factors in the regression, however, caribou density was not.

Food Availability (Consumption Rates) and Carcass Utilization

Assuming that male, female, and calf caribou weighed 96, 76, and 36 kg, respectively (J. Davis, unpubl. data), and that

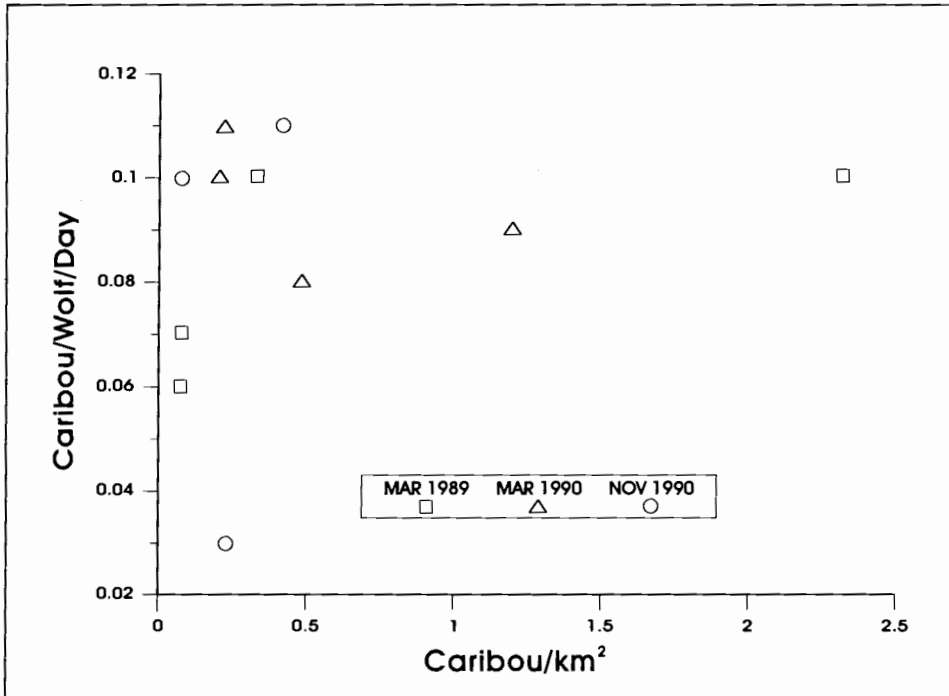


Fig. 1 Rates at which wolves killed caribou as a function of caribou density in March 1989, March 1990, and November 1990 in Gates of the Arctic National Park.

caribou kills were composed of 13% calves, 43.5% cows, and 43.5% bulls in March, and 35% calves, 32.5% cows, and 32.5% bulls in November (see Prey Selection), each caribou killed represented approximately 79.5 kg live weight in March, and 68.5 kg in November. We assumed adult and calf moose weighed 370 and 150 kg, respectively (Franzmann et al. 1978), and sheep kills weighed 50 kg (Bunnell and Olsen 1976), and these species were 75% and 90% consumable (Sumanik 1987). If caribou bulls, cows, and calves were 85%, 87%, and 95% consumable (Sumanik 1987), wolves had approximately 4.1–12.0 kg/wolf/day available with an overall unweighted mean of 6.9 (SD = 2.4, n = 12). Mean food availability was 8.2, 6.6, and 5.7 kg/wolf/day for March 1989, March 1990, and November 1990, respectively ($F = 1.14$, d.f. = 11, $P = 0.36$).

Wolf Activity

Travelling pack size ranged from 2–14.3 wolves (Table 2). We made 2,003 observations of individual wolves during daylight hours. Wolves were sleeping or resting in 48.8% of the observations, walking 32.1%, feeding 9.8%, engaged in social behaviors 6.8%, and running 2.5%. There was no relationship between the frequency of these behaviors and food availability.

Discussion

Prey Selection

Our data suggest that estimating prey selection patterns from systematic observation may be misleading when prey size is variable and backtracking is not feasible. In this study a high proportion of kills were located via backtracking. The

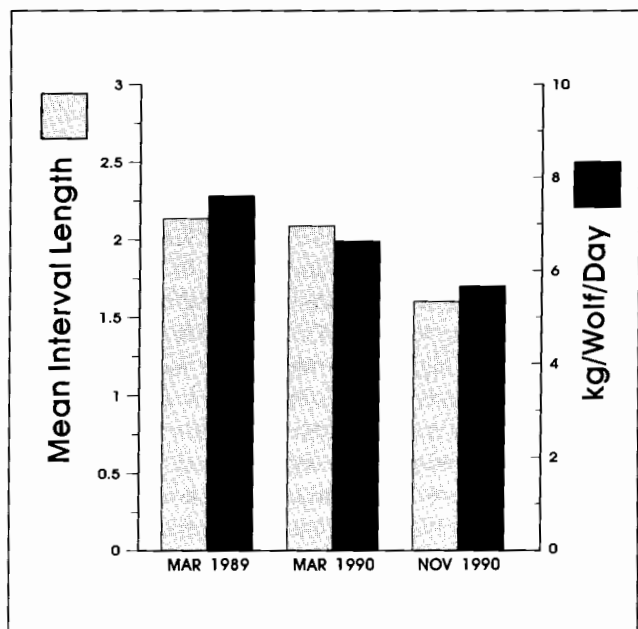


Fig. 2 Mean length of intervals between kills and weighted mean food availability (kg/wolf/day, see text for assumptions on prey biomass) for wolves in Gates of the Arctic National Park. Cumulative snowfall was greatest in March 1989, and least in November 1990.

amount of food available from a kill was a significant factor in explaining the length of the interval until the next kill. For example, with infrequent monitoring and without backtracking, wolves might kill and consume numerous caribou for each one detected, while every moose kill might be detected (Carbyn 1983b, Ballard et al. 1987, Fuller 1989). Prey with

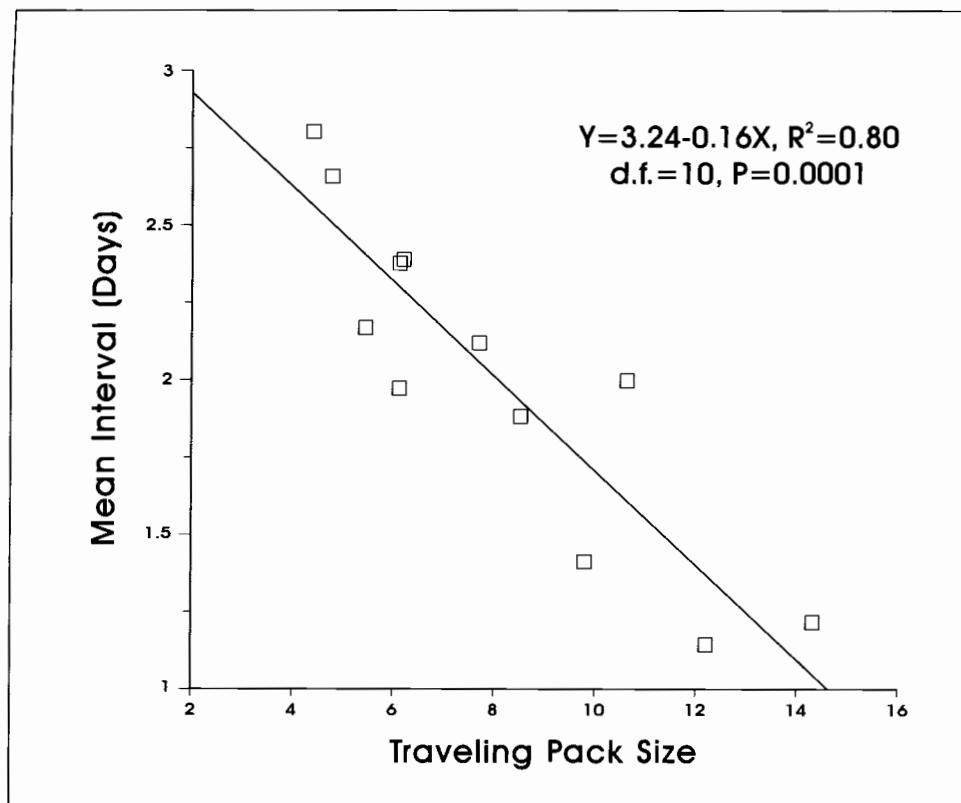


Fig. 3 Relationship of kill rate to pack size. Each data point represents the mean length of intervals between kills for four packs of wolves in March 1989, March 1990, and November 1990, in Gates of the Arctic National Park.

body mass larger than can be consumed by a pack in one feeding may be overrepresented when wolves rest near these kills between meals. Pack size, as it influences handling time, may also affect observability of kills. Wolves were most commonly observed sleeping and resting in this study (49%), and on Isle Royale, Michigan (48%) (Peterson and Page 1988). The high proportion of kills located by backtracking in this study is consistent with our conclusion that wolves frequently rested away from caribou kills.

Wolves can be highly selective predators. Carbyn (1974) reported mule deer (*Odocoileus hemionus*) were the primary prey of wolves in Jasper National Park, Alberta despite elk (*Cervus elaphus*) being three times more abundant. Carbyn (1983) also identified white-tailed deer (*Odocoileus virginianus*) as the "optimum" prey in Riding Mountain National Park, Manitoba. In that study, elk were most abundant and most consumed, but deer were consumed at a higher rate relative to available biomass. Gauthier and Theberge (1986) noted members of the Burwash caribou herd were consumed disproportionately relative to the available biomass of moose except during the calving season. However, their estimates of consumption were derived from fecal analyses employing the equations developed by Floyd et al. (1978), and relative abundance of caribou and moose was derived from censuses conducted in previous years. No data were presented on the actual distribution and availability of caribou within the home ranges of the two study packs. Burkholder (1959) believed that wolves showed no preference for either caribou

or moose in south-central Alaska, but that use was proportional to availability. Other authors have indicated caribou as highly preferred prey for wolves (Holleman and Stephenson 1981, Gasaway et al. 1983), although information regarding the relative availability of other ungulate prey was lacking.

In this study, wolves utilized caribou even when moose were numerically more abundant. We saw no evidence of prey switching because of differences in relative ungulate abundance. The trends in prey selection observed in our study may be due to less risk associated with hunting caribou (Haugen 1987), and higher profitability in killing caribou once potential prey were located. For example, adult moose in our study area occurred at low densities and may have been in excellent condition. Likewise, sheep were at low enough densities to remain in available escape terrain, resulting in low vulnerability of these species. Increased use of sheep during November 1990 may have resulted from increased vulnerability due to changes in distribution, condition, or vigilance associated with the ongoing rut. Similarly, deep snow may have increased moose vulnerability in March 1989 (Peterson 1977, Mech 1987), but the sample sizes were too small to draw firm conclusions.

Caribou, however, may have been vulnerable due to the combination of deep snow and mountainous, rough terrain. Caribou groups were generally observed on, or near, ridges that were windblown and had little or hardpacked snow cover. Tracks and locations of kill sites indicated that wolves

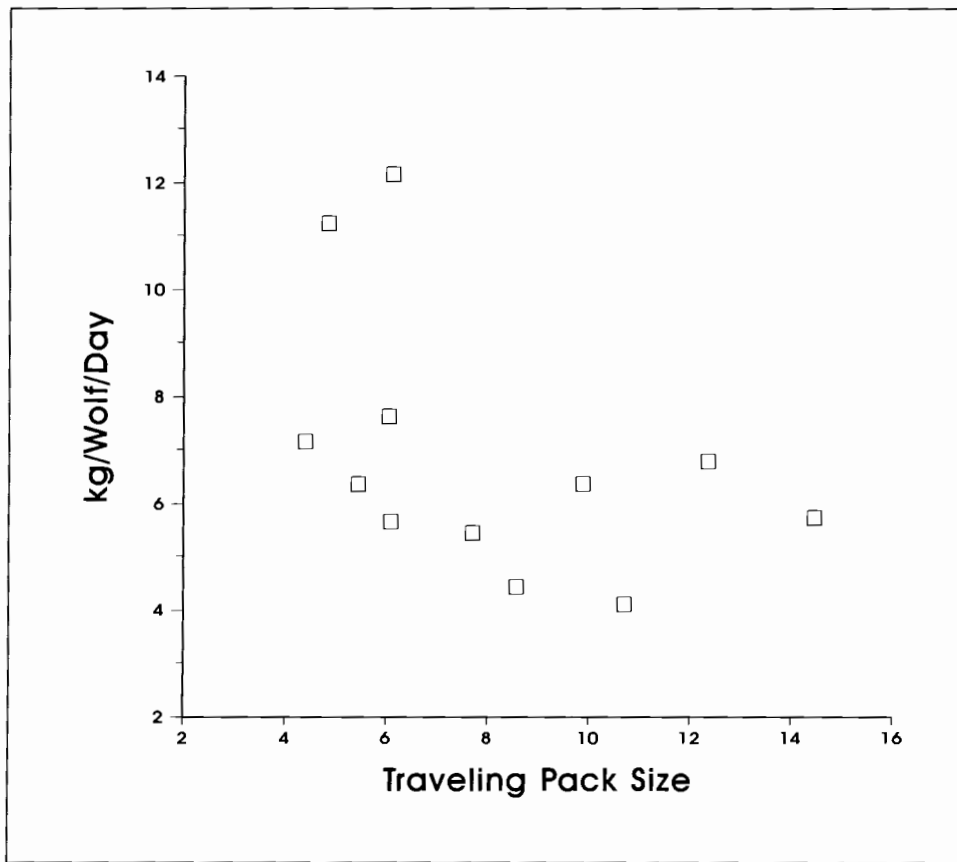


Fig. 4 Relationship between food availability and pack size for four packs of wolves in March 1989, March 1990, and November 1990 in Gates of the Arctic National Park.

chased caribou from these ridges into deep snow, rough terrain, and relatively dense vegetation. Because wolves often made multiple kills of caribou in single attacks, the profitability of hunting caribou increased. Further, even the lowest food availability (4.1 kg/wolf/day) indicated wolves were on a suitable plane of nutrition for reproduction (compare to 3.2 kg/wolf/day: Mech 1977c) without the risk of hunting moose (Haugen 1987) or the difficulty of hunting sheep (Sumanik 1987).

The strong preference sometimes shown by wolves for certain ungulate prey poses numerous questions for current wolf-prey theory, particularly, how widespread this phenomenon is, and how it influences wolf-prey dynamics. We analyzed data from multiple-prey systems ($n = 17$, excluding newly established and manipulated systems) compiled by Fuller (1989, Appendix B) to address these questions. For ungulate prey, only deer and caribou have been suggested as strongly preferred by wolves (Mech and Frenzel 1971a, Carbyn 1974, 1983a,b, Mech 1977c, Holleman and Stephenson 1981, Gauthier and Theberge 1986, Potvin et al. 1988). We assumed they were the preferred prey in systems in which they occurred and as opposed to other ungulates [i.e., moose, elk, bison (*Bison bison*), mountain goat (*Oreamnos americana*), and mountain sheep], even though those ungulates may have constituted most of the diet of wolves. We used multiple-regression analysis to detect any influence of

preferred prey (deer and caribou) on wolf density by including preferred prey and alternate prey ungulate biomass indices as separate independent variables. This expanded model explained significantly more variation in wolf density ($\underline{Y} = 0.006 * \text{Preferred Prey UBI} + 0.003 * \text{Alternate Prey UBI} + 4.08$, full model $\underline{R}_a^2 = 0.86$, $\underline{F} = 17.2$, $\underline{P} < 0.001$) than total ungulate biomass index alone (reduced model $\underline{r}^2 = 0.72$). These results support the observed preference for deer and caribou and indicate that the abundance of preferred prey strongly influences wolf density.

Models of wolf predation behaviour should be viewed with caution when encounter rates are assumed to be the primary determinant of prey selection. Clearly, wolves did not make immediate changes in prey selection simply because of rates at which they encountered different species of ungulate prey. Relative abundance, however, may have influenced selection among sex and age classes, such as the increased use of caribou calves versus adults in November.

Kill Rates, Food Availability, and Predation Rates

Wolves may have had more food available per wolf when snow was deepest (March 1989) even though kill rate was similar to March 1990. The differences in food availability, although not significant, were due to the larger number of

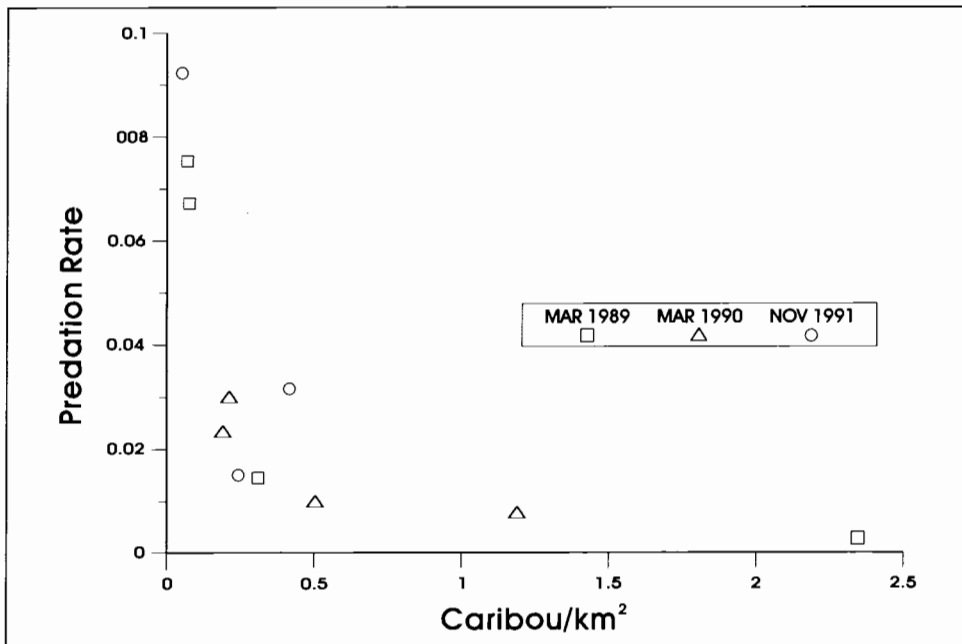


Fig. 5 Relationship between mortality rates due to wolf predation and caribou density in four wolf pack territories in March 1989, March 1990, and November 1990 in Gates of the Arctic National Park.

moose killed in March 1989 (Table 2), and the increased use of calves in November 1991.

The positive relationship between pack size and kill rate (Fig. 3) is similar to that reported by Messier and Crete (1985), Ballard et al. (1987), and Sumanik (1987), but contrary to Haber's (1977) conclusion that pack size had little influence on handling or search time. Hayes et al. (1991) concluded that small packs killed as often as large packs in southwest Yukon. Their data consisted of numerous pairs of wolves killing mostly moose where scavenging was high. Our data represent only larger packs killing mostly caribou, and the effects of scavengers at our study area were probably less than that reported by Hayes et al. (1991).

Snow depth, season, and prey availability were not significantly associated with kill rates suggesting: 1) these factors had little influence on the ability of wolves to kill caribou; or 2) that wolves were at or near food satiation in many cases. This latter contention is supported by the relationships between travelling pack size, kill rate, and food availability. Although big packs killed at a faster rate ($P < 0.0001$) (Fig. 3), those packs had no more food per wolf than small packs ($P > 0.05$) (Fig. 4). In addition, no difference in frequency of resting or social behaviors among packs, and little correlation between caribou density and interval length suggest that, of search time and handling time, only handling time explained variation in interval length in this study. Individual wolves living in established packs in open systems may often be at or near satiation because extremes in food availability would elicit numerical responses (Zimen 1976, Mech 1975, Packard and Mech 1980, Page 1989).

For wolves in Gates of the Arctic National Park, changes in dispersal rates (Adams et al. 1989a), survival, and possibly immigration (Packard and Mech 1980, Ballard et al. 1987)

could facilitate immediate numerical responses to changes in per capita food availability. In other words, the effects of functional responses on population dynamics may be short-lived. In this study, mean food availability (0.16 kg/kg wolf/day) was similar to that for wolf-moose and/or caribou systems representing a wide range of prey densities in North America (Boertje et al. 1992a).

Clearly, in the short periods of observation in Gates of the Arctic National Park, wolves killed caribou at high rates regardless of the number of caribou within a pack's territory. Spatial distribution of caribou should therefore be an important influence on predation rate (proportion killed per day) on winter ranges where wolves are territorial. Indeed, predation rate decreased markedly with increasing prey density (Fig. 5). This effect should be a strong influence on grouping behavior in caribou.

Acknowledgments

This work was funded by the National Park Service (NPS) Natural Resource Preservation Program. We would like to thank A. Lovaas (NPS-Alaska Region), and the staff at Gates of the Arctic National Park and Preserve for their support. Numerous people at the Alaska Department of Fish and Game provided advice and support, especially R. Stephenson, W. Gasaway, D. Reed, J. Davis and R. Boertje. Field work was conducted by J. Alderson, T. Burch, J. Dale, K. Faber, T. Meier, M. Masteller, and B. Shults, and pilots R. Warbelow, S. Hamilton, B. Lentsch, D. Miller, and B. Sewell. We thank P. and M. Shanahan for their hospitality and use of their cabin. A. Lovaas, E. Follmann, D. Klein, R. Stephenson and D. Mech provided useful comments on earlier drafts of this manuscript.