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Wolf-caribou relationships in a multiple ungulate prey ecosystem

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WOLF - CARIBOU RELATIONSHIPS IN A MULTIPLE UNGULATE PREY ECOSYSTEM

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

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for the Degree of

MASTER OF SCIENCE

By

Bruce W. Dale, B.A.

Fairbanks, Alaska

May 1993

WOLF - CARIBOU RELATIONSHIPS IN A MULTIPLE UNGULATE PREY ECOSYSTEM

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WOLF - CARIBOU RELATIONSHIPS IN A MULTIPLE UNGULATE PREY ECOSYSTEM.

Abstract: Winter wolf (Canis lupus) predation and functional response in wolf - caribou (Rangifer tarandus) dynamics were investigated in a multiple ungulate prey ecosystem in Gates of the Arctic National Park, Alaska. Prey selection, prey availability, prey switching, kill rates, and food availability for 4 wolf packs were estimated in March 1989, March 1990, and November 1990. Estimates for these study periods reflected near record, average, and early winter snow conditions, respectively. Wolves killed predominately caribou even if moose (Alces alces) or Dall sheep (Ovis dalli) were more abundant. Prey selection varied with study period; however, per wolf kill rates and food availability did not. Length of intervals between kills was correlated with pack size and the biomass of the previous kill. Kill rates indicated a destabilizing Type II functional response. Modeling with a linear numerical response revealed wolf predation to be an increasingly important limiting factor at low caribou densities. However, little potential for regulation of caribou by wolves was observed.

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Preface

In 1985, the U.S. National Park Service in cooperation with the Alaska Department of Fish and Game began a study of wolf ecology and demography in Gates of the Arctic National Park in the central Brooks Range, Alaska. One of the initial objectives of this study was to evaluate wolf-prey relationships. I am indebted to NPS Wildlife Research Biologist Layne Adams and NPS Regional Chief Scientist Al Lovaas for allowing me to consider an aspect of wolf-prey relationships as a Master's project.

The following thesis is composed of two of five manuscripts generated from this effort. Layne G. Adams and R. Terry Bowyer were co-authors on both manuscripts. Chapter 1, a nuts and bolts assessment of winter wolf predation in that system, has been submitted and accepted for the refereed proceedings of the Second North American Symposium on Wolves. Chapter 2 employs a modeling approach to evaluate empirical data on the functional response of wolves and the role of predation in regulation of caribou populations. This second chapter has been submitted to the Journal of Animal Ecology.

Chapter 1.

Winter wolf predation in a multiple ungulate prey system, Gates of the Arctic National Park and Preserve, Alaska

WINTER WOLF PREDATION IN A MULTIPLE UNGULATE PREY SYSTEM, GATES OF THE ARCTIC NATIONAL PARK AND PRESERVE, ALASKA

Abstract: I investigated patterns of winter wolf predation, including prey selection, prey switching, kill rates, carcass utilization, and consumption rates for 4 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, 7 moose, and 5 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 ($\underline{x}$=2.0, SD=1.6) and did not vary between study periods. Pack size and species killed explained significant variation in the length of intervals between kills. Although caribou density varied nearly 40-fold between pack territories, it had little influence on predation characteristics except at very low densities, when kill rates 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 1978, Bergerud 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, Bergerud 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, primarily 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 also affect utilization of other available ungulate prey, such as Dall Sheep (Ovis dalli dalli) and moose. In multiple prey systems, however, 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, in the central Brooks Range, Alaska, I determined prey selection and kill rates in early and late winter. I predicted that late winter and deep snow conditions would result in higher kill rates due to increased vulnerability of caribou, and that wolves would switch to other ungulate prey when caribou were scarce.

I evaluated the influence of caribou abundance, snow depth, and season on prey selection and kill rates. Winter 1988-89 witnessed a near record snowfall, whereas winter 1989-90 was near average. Therefore, characteristics of predation during March 1989 and March 1990 should reflect differences caused by variation in late-winter snow depth. Further, the November 1990 study period represents much shallower early winter snow depths. Variation in predation characteristics among the November and March study periods may also be due to seasonal variation in prey condition.

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 km^2. Gates of the Arctic National Park lies north of the Arctic Circle, and 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 13 to 45 cm, and yearly snowfall from 89 to 203 cm. Average minimum and maximum temperatures range from -34° C to 21° C (NPS 1987).

Cumulative snowfall through 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 through March 1990 was also above average (218 cm); however, 79 cm fell during March. Cumulative snowfall through November 1990 was 91 cm. I 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 km^2 (Adams and Stephenson 1986), a density typical of northern wolf populations (Chapman and Feldhamer 1982). Wolves in the study area are nonmigratory. Of the 4 packs observed in this study, only one was harvested. The Iniakuk Pack (IP) was reduced by 2-3 wolves each year due to 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/km^2 (Singer 1984) and 0.12/km^2 (this study), respectively, whereas caribou are seasonally abundant. Although some 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, ADF&G, pers. comm.), migrates southward and eastward toward the study area in August - September, and some winter there. WAH caribou do not show annual fidelity to winter ranges, but do not change ranges during a 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 km^2 were surveyed with a search intensity of about 0.5 minutes/km^2. The sightability correction factor was determined by counting 6 or 7 units before randomly selecting 1 survey unit to be recounted at a higher survey intensity (2 minutes/km^2). 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) were obtained in late winter (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/km^2 on suitable habitat (Singer 1984, 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 at least daily during each 30-day period, except for 1 day in March 1990, and 1 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 1983). Upon visually locating wolves, the pelage color, number, and activity of individual wolves were recorded. The immediate area was searched to locate additional wolves or the presence of kills. Local vegetation, topography, and snow conditions were recorded. Whenever possible packs were back-tracked 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 USGS 1:63,360 or 1:250,000 scale topographic maps.

Ground investigation of 110 of 177 total kills was made within 3 - 14 days after wolves abandoned the carcasses. At kill sites I verified species of the kill, and where sufficient evidence remained, I identified or collected specimens (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 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. Because pack members are not always found together due to temporary or permanent dispersal, mortality, or fragmentation into subgroups for hunting, wolf groups were quantitatively described as traveling pack size (Messier 1985). This measure constitutes the mean number of wolves seen in each pack during the study period. Mean interval length (days/kill/pack) was 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 traveling 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 (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). Due to 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 I located by backtracking wolves to the previous location.

RESULTS

Prey Availability and Prey Selection

Caribou density within pack territories ranged from 0.06 - 2.34 caribou/km^2, while moose density ranged from 0.08 - 0.24 moose/km^2 (Table 1). Wolves killed primarily caribou (93%) during the study (Table 2), but prey selection was not independent of study period ($\underline{X}^2=12.79$, d.f.=4, $\underline{P}=0.012$). The relatively 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 ($\underline{X}^2<0.001$, d.f.=1, $\underline{P}=0.98$) 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.

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.

STUDY PERIOD	PACK	CARIBOU/KM^2	MOOSE/KM^2	WOLVES
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[a]
	Unakserak	0.41	0.12	13
	Pingaluk	0.24	0.13	11

NA=No prey surveys were conducted.

[a] Three pups were harvested early in the rate estimation period reducing pack size to 7 wolves.

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	TRAVELING PACK SIZE	RATE EST PERIOD (DAYS)	KILLS CARIBOU	KILLS MOOSE	KILLS SHEEP	CARIBOU/ WOLF/DAY	KG/WOLF/ DAY
March 1989							
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
March 1990							
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
November 1990							
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

The resulting age composition of known-age caribou kills was dependent on season ($\underline{X}^2$=4.94, d.f.=1, $\underline{P}$=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 back-tracking the wolves toward their location from the previous day. Correlation showed no relationship between kill rate and the proportion of kills located by backtracking ($\underline{P}$=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 ($\underline{SD}$=0.024, N=12) caribou/day. Caribou density had little affect on rates at which wolves killed caribou; however, most of the variation in kill rate occured at lower densities (Fig. 1). I excluded data from the Pingaluk pair of wolves for March 1989, when only 2 kills were documented during the rate estimation period. The pair killed an adult moose two days after the rate estimation period ended. Including this kill would double the daily available ungulate biomass for this pair.

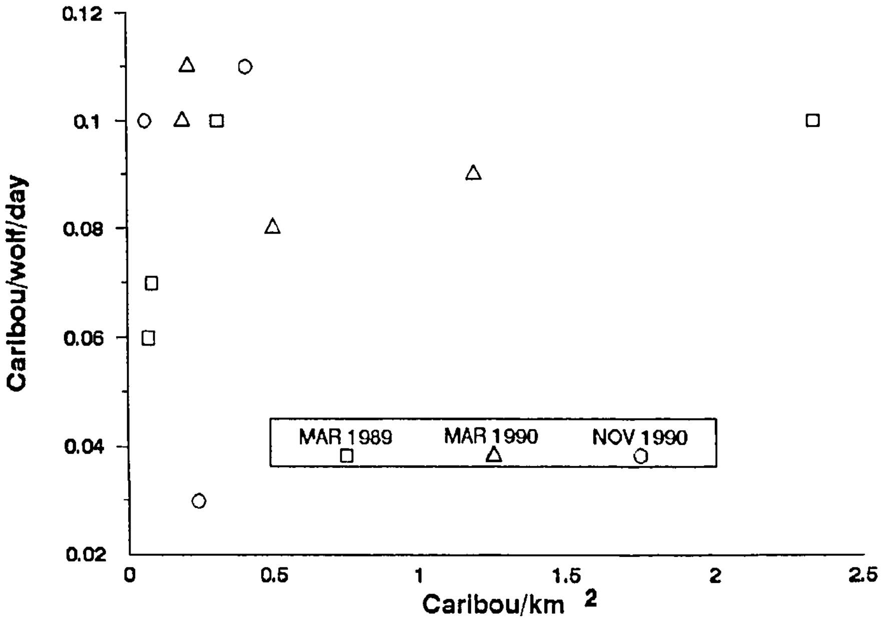

Fig. 1. Rates at which wolves killed caribou as a function of caribou density in March 1989, March 1990, and November 1990 in Gates of the Arctic National Park.

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 traveling 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 0 - 8 days with a mean of 2.0 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 traveling pack size, caribou density, and food availability (number and species of ungulates killed at each successful attack) were held as covariates.

Because kill rates among packs were not significantly different, packs were pooled to evaluate the effects of snow and season. The snow-season factor had 3 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) when traveling pack size, caribou density, and food availability were held as

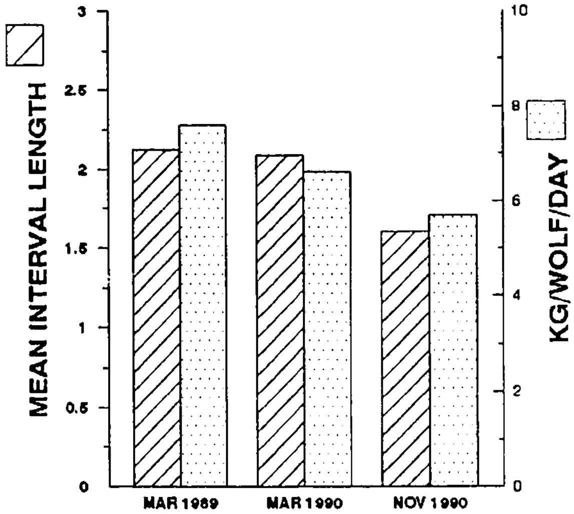

Fig. 2. Mean length of intervals between kills and weighted mean food availability (kg/wolf/day, see text for assumptions on prey biomass) for wolves in Gates of the Arctic National Park. Cumulative snowfall was greatest in March 1989, and least in November 1990.

covariates (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. Traveling 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 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. I assumed adult and calf moose weighed 370 and 150 kg, respectively (Franzmann et al. 1978), and sheep kills weighed 50 kg (Bunnel 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

Traveling 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

My 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, and the 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 (Fuller 1989). Further, prey with body mass larger than can be consumed by a pack in one feeding may be over-represented 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 (48%) (Peterson and Page 1988). The high proportion of kills located by backtracking in this study, despite intensive observation, is consistent with our conclusion that wolves frequently rested away from caribou kills.

Wolves can be highly selective predators. In our study, wolves killed caribou even when moose were numerically at least twice as abundant. Carbyn (1974) reported mule deer (Odocoileus hemionus) were the primary prey of wolves in Jasper National Park despite elk (Cervus elaphus) being three times more abundant. He also (Carbyn 1983) identified white-tailed deer (Odocoileus virginianus) as the "optimum" prey in Riding Mountain National Park. In that study, elk were most abundant and most consumed, but deer were consumed at a higher rate relative to available biomass. For caribou, Gauthier and Theberge (1986) noted members of the Burwash 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 availabilities of caribou and moose were 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. In contrast, Burkholder (1959) believed that wolves showed no preference for either caribou or moose in Southcentral Alaska, but that use was proportional to availability. Other authors have indicated caribou as a highly preferred prey for wolves (Holleman and Stephenson 1981, Gasaway et al. 1983), although information regarding the relative availability of other ungulate prey was often lacking.

In this study, wolves clearly utilized caribou even when moose were more abundant. I saw no evidence of prey switching due to 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 are too small to draw firm conclusions.

Caribou, however, may have been highly vulnerable due to the combination of deep snows 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 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 them 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 1977) 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 is this phenomenon, and how does it influence wolf-prey dynamics? I analyzed data from multiple-prey systems (N=17, excluding newly established and manipulated systems) compiled by Fuller (1990, Appendix B) to address these questions. For ungulate prey, only deer and caribou have been suggested as strongly preferred by wolves (Mech and Frenzel 1971, Carbyn 1974, 1983, Mech 1977, Holleman and Stephenson 1981, Gauthier and Theberge 1986, Potvin et al. 1988). I assumed they were the preferred prey in systems in which they occurred and that other ungulates (moose, elk, bison [Bison bison], mountain goat [Oreamnos americana] and mountain sheep) were alternate prey even though those ungulates may have constituted most of the diet of wolves. I used multiple-regression analysis to detect any influence of preferred prey on wolf density by including preferred prey and alternate prey ungulate biomass indices (UBI) as separate independent variables. This expanded model explained significantly more variation in wolf density ($\hat{Y}$=0.006*Preferred Prey UBI+0.003*Alternate Prey UBI+4.08, full model $R_a^2=0.86$, $F=17.2$, $P<0.001$) than total ungulate biomass index alone (reduced model $r^2=0.72$). These results support the observed preference of wolves for deer and caribou and indicate that the abundance of preferred prey strongly influences wolf density.

Models of wolf predation behavior 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 due to 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 vs. 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, are due to the larger number of moose killed in March 1989 (Table 2) and the increased use of calves in November 1991.

The negative relationship between pack size and interval length 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 that: 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 traveling pack size,

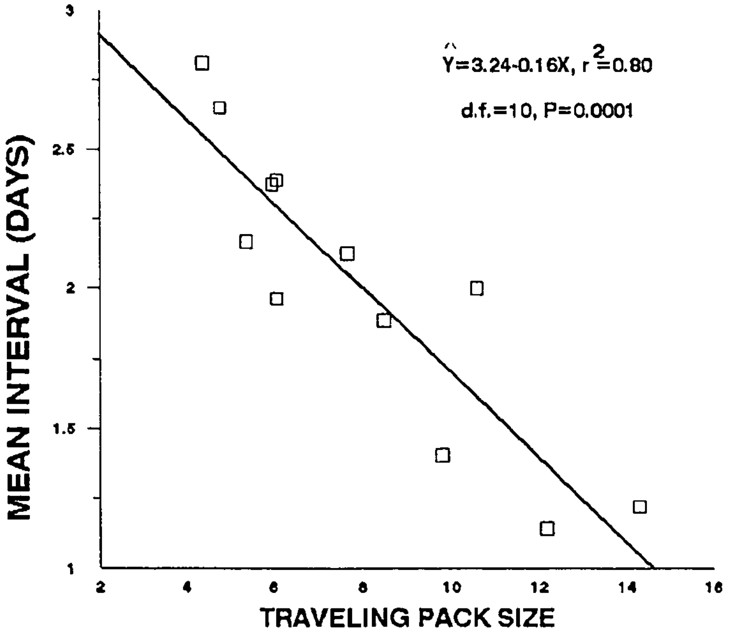

Fig. 3. Relationship of kill rate to pack size. Each data point represents the mean length of intervals between kills for 4 packs of wolves in March 1989, March 1990, and November 1990 in Gates of the Arctic National Park.

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 there was no difference in frequency of resting or social behaviors among packs, suggesting that, of search time (hunting efficiency) and handling time, only handling time explained variation in interval length in this study. In an open system, individual wolves living in established packs 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). In this study, mean food availability (0.16 kg/kg wolf/day) was similar to that for wolf-moose-caribou systems representing a wide range of prey densities in North America (Boertje et al. 1992).

For wolves in Gates of the Arctic National Park, changes in timing in the considerable dispersal rates (Adams et al. 1989) could facilitate immediate numerical responses to changes in food availability. This theory supports the use of wolf:prey ratios in estimating the effects of wolf predation on ungulate prey populations because each wolf eats a relatively constant amount of food. If food availability changes, wolf populations respond numerically through changes in dispersal rates, survival, or possibly immigration (Packard and Mech 1980, Ballard et al. 1987).

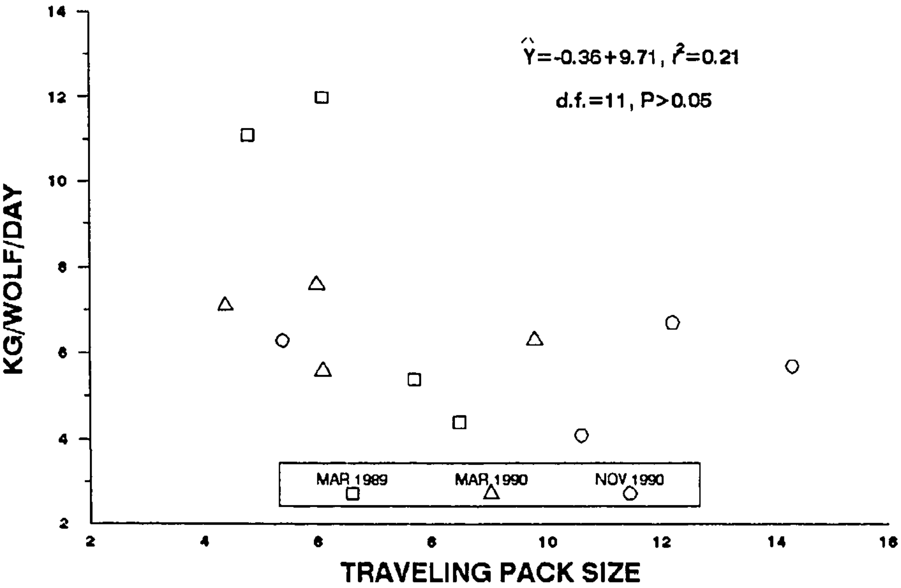

Fig. 4. Relationship between food availability and pack size for 4 packs of wolves in March 1989, March 1990, and November 1990 in Gates of the Arctic National Park.

In multiple prey systems, however, the use of wolf:prey ratios to evaluate effects of wolf predation on prey populations is valid only if prey selection patterns are known.

It is not clear whether use of estimates of kill rate derived from direct observation for hypothesis testing is practical. Numerous intervals between kills must be recorded to produce a reasonable estimate. Although much of the variation in interval length can be explained, a substantial amount remains even for large sample sizes. In many cases, such as for large prey, adequate sample sizes will require long sampling periods (Fuller and Keith 1980, Ballard et al. 1987) and, as discussed, variation in food availability over longer periods may result in numerical responses.

Clearly, in the short periods of observation in Gates of the Arctic National Park, wolves killed caribou at fairly high rates regardless of the number of caribou within a pack's territory. Spatial distribution of caribou should therefore be an important influence on survival. Indeed, the predation rate (proportion killed per day) decreased markedly with increasing prey density (Fig. 5). The declining predation rate becomes asymptotic at about 0.5 caribou/km^2, similar to Bergerud's (1980) threshold for

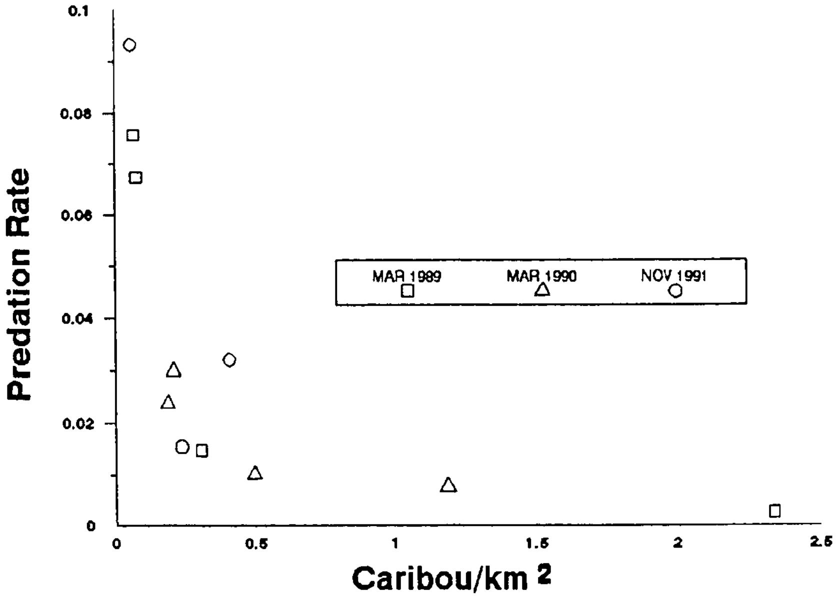

Fig. 5. Relationship between mortality rates due to wolf predation and caribou density in 4 wolf pack territories in March 1989, March 1990, and November 1990 in Gates of the Arctic National Park.

caribou populations to escape wolf predation. At densities less than 0.5 caribou/km^2, wolf predation is expected to be an increasingly important factor in caribou population dynamics.

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Chapter 2.

FUNCTIONAL RESPONSE IN WOLF - BARREN GROUND CARIBOU DYNAMICS IN A MULTIPLE - PREY ECOSYSTEM

FUNCTIONAL RESPONSE IN WOLF - BARREN GROUND CARIBOU DYNAMICS IN A MULTIPLE PREY ECOSYSTEM

SUMMARY

(1) I investigated the functional response of wolves (Canis lupus) to varying abundance of ungulate prey to test the hypothesis that switching from alternate prey to preferred prey results in potential regulation of a caribou (Rangifer tarandus) population at low densities.

(2) I determined prey selection, kill rates, and prey abundance for four wolf packs during three 30-day periods in March 1989, March 1990, and November 1990, and created a simple model to evaluate the potential for numerical and functional responses of wolves to regulate caribou populations.

(3) I observed a quickly decelerating type II functional response that, in the absence of a numerical response, implicates an anti-regulatory effect of wolf predation on barren-ground caribou dynamics.

(4) There was no potential for regulation caused by the "multiplicative effect" of increasing functional and numerical responses at low prey densities because the equation for the linear numerical response employed in the model had a positve Y-intercept. This resulted in high wolf:prey ratios at low prey densities which precluded the

multiplicative effects of an increasing functional response.

(5) Density-dependent variation in caribou vulnerability can have a regulatory effect when prey switching occurs below a range of prey densities where population trend is negative, regardless of the type of functional response.

(6) When 2 or more predators have destabilizing functional responses, small reductions in predation by a single predator may have disproportionately large effects on the total predation rate.

INTRODUCTION

Wolves are known to be important limiting factors in growth of populations of northern ungulates. Frequently, wolves are reported to regulate ungulate populations at levels below the nutrient-climate ceiling (Bergerud 1980, Gasaway et al. 1983, Messier 1985, Ballard et al. 1987). The distinction between limitation and regulation, however, is rarely recognized in wolf-prey studies and, where regulation is implied, the mechanism is seldom demonstrated. In this analysis, I employ terminology similar to Messier (1991). Predation as a limiting factor simply implies that wolf predation is, at least partially, an additive source of mortality in the prey population. Numerous studies have identified wolf predation as a significant limiting factor in ungulate population dynamics (Bergerud 1986, Mech 1987, Van Ballenberghe 1987, Ballard 1991). A regulating factor, however, keeps prey numbers within a given range, and therefore requires a density-dependent feedback mechanism for the predator, i.e. the limiting effect must increase when prey numbers increase and lessen when prey numbers decline. Without this property, wolves, or any other single limiting factor, cannot regulate a population. Even with this property, regulation may not occur; the combined effect of all limiting factors and the potential rate of increase of the prey population will collectively determine population trend.

Understanding the effects of all mortality agents at one time is usually not possible. Therefore, in evaluating the potential for predators to regulate a prey population, it is prudent to attempt to identify ranges of prey population density where predation is potentially stabilizing. Hereafter, I will refer to stability as meaning a mortality agent that has a potentially regulating influence on a population over some range of prey densities, and that this influence may or may not result in regulation (Oaten and Murdoch 1975a).

Understanding regulating factors is fundamental to understanding wolf-prey relationships. Knowledge of regions of prey densities where wolves have potentially regulating influence on prey will be important to wildlife managers in determining and maintaining goals for ungulate populations. For example, the range of densities where wolves have a regulating influence may determine the practicality of releasing prey populations from low-density equilibria. The treatment of this property in wolf predation also is fundamental to behavior of models predicting the effects of wolf reintroductions.

This paper examines empirical data to detect regions of wolf-induced stability on a caribou population in a multiple ungulate prey system (i.e., a system where more than one of the ungulate prey species alone would support a wolf population). In addition, I evaluate a simple model constructed to evaluate the potential for wolf regulation of the caribou population in this system. The foundation for this analysis is that characteristics of wolves that are potentially able to induce stability fall into two general categories; functional and numerical responses (Solomon 1949). Numerical responses, changes in wolf densities in response to changes in prey densities, as wolf:prey ratios, are the common basis for investigating the effects of wolf predation (Mech 1970, Gasaway et al. 1983, Ballard et al. 1987). Recently, however, there has been increasing interest in the role of functional response in wolf - prey dynamics (Theberge 1990, Sinclair 1990).

The functional response

Predation behavior is usually quantified by kill rate, the number of a species of prey killed per wolf per unit time. Functional responses are changes in kill rate that are related to changes in prey abundance. If wolves respond to an increase in prey by killing a higher proportion of that population, wolf predation has a stabilizing influence. When kill rate is plotted as a function of prey density, the above relationship is represented by a region of positively increasing slope; (plotted as predation rate, the potentially regulating range is identified by a positive slope). Because kill rate will plateau at some level, the result is a sigmoidal shaped curve described by Holling (1966) as the Type III functional response (Fig. 1). Other shapes of functional response curves are potentially destabilizing such as the well-known response described by Holling's (1966) disc equation (Fig. 2). Such responses are actually destabilizing if predation is largely additive mortality; however, the distinction is valid in that these responses have no stabilizing potential (Oaten and Murdoch 1975a). The Type II curve is prevalent in studies of functional response, but these studies have been limited to invertebrates and small mammals (Taylor 1984).

Interest in the Type III functional response is great because it can constitute a stabilizing influence despite

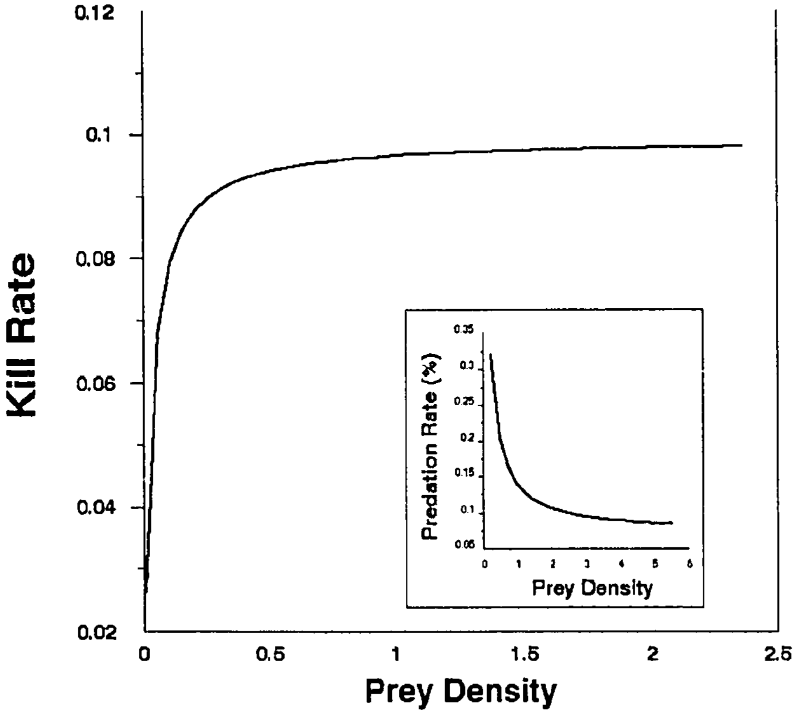

Fig. 1. Example of a type III functional response. The region of positively increasing slope results in a density-dependent predation rate (kill rate/prey density) at low densities (inset).

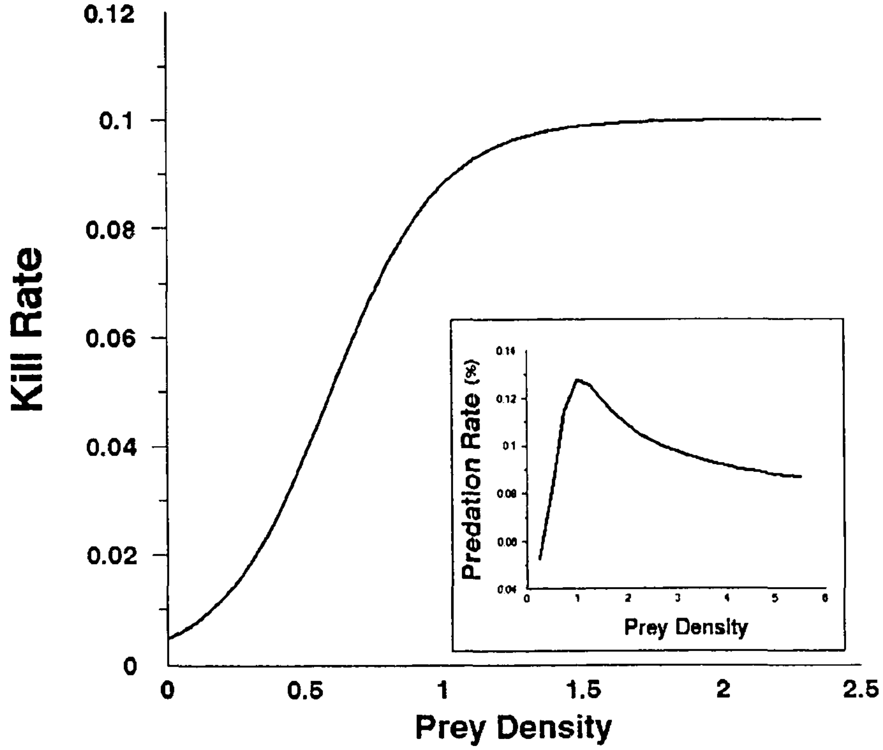

Fig. 2. Example of a type II functional response. Predation rate (kill rate/prey density;inset) is inversely density-dependent, and is destabilizing if predation is a partially additive source of mortality.

destabilizing, lagging, or neutral numerical responses. Learning (Tinbergen 1960, Holling 1966), bioenergetic optimization of search effort (Sih 1984, Dunbrack and Giguere 1987), prey refugia (Taylor 1984), risk (Abrams 1982), and vulnerability (Holling 1965, Wood and Hand 1984) have been proposed as the biological basis for the Type III response of a predator to changes in prey availability. Usually, however, predators having the opportunity to switch between prey types of similar profitability, (i.e., bioenergetic optimization of prey selection), are thought to have sigmoidal functional responses (Murdoch 1969, Oaten and Murdoch 1975b). A sigmoidal functional response, however, is not requisite of prey-switching predators (Charnov 1973, Oaten and Murdoch 1975b).

Study design

In Gates of the Arctic National Park in the central Brooks Range of Alaska, USA, caribou, Dall sheep (Ovis dalli), and moose (Alces alces) are all preyed upon by wolves, although caribou appear to be the primary prey in much of the area (Stephenson and James 1982, Adams et al. 1989). Caribou abundance and distribution, however, can be quite variable both spatially and temporally. A study of wolf population ecology in the park and observed local trends in distribution of the Western Arctic Caribou Herd provided conditions for a natural experiment evaluating the functional response of wolf packs to variation in caribou abundance where moose and sheep numbers remained relatively constant. I hypothesized that wolves would readily switch to moose and sheep if caribou were scarce. Further, I predicted that this switching would result in a sigmoidal (Type III) functional response, and if this response was robust, wolves would potentially regulate the caribou population over some range of caribou densities. In this analysis I evaluate the observed functional response, and I investigate the potential of functional response to produce stability when incorporated with expected numerical responses.

STUDY AREA AND METHODS

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 km^2. Gates of the Arctic National Park lies north of the Arctic Circle; 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 ranges from 13 to 45 cm, and yearly snowfall from 89 to 203 cm. Average minimum and maximum temperatures range from -34° C to 21° C (NPS 1987).

The central Brooks Range is characterized by wide river valleys and steep rugged mountains. Boreal forest (taiga) occurs extensively along the southern border of the 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 the northern drainages (NPS 1987).

Wolves are distributed throughout Gates of the Arctic National Park at approximately 7.4 wolves/1000 km^2 (Adams and Stephenson 1986), a density typical of northern wolf populations (Chapman and Feldhamer 1982). In addition to wolves, predators of ungulates in the study area 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 species consist of caribou, Dall sheep, and moose. Sheep and moose are locally abundant, whereas caribou are seasonally abundant. Although some caribou are usually present, their use of the study area is primarily limited to autumn and winter (Cameron and Whitten 1979). The Western Arctic Herd (WAH), estimated at 415,000 caribou in 1990, migrates southward toward the study area in August through September, and some caribou may use the study area as winter range. WAH caribou do not show annual fidelity to winter ranges, but do not change ranges during a particular winter (Valkenburg et al. 1983). Small prey for wolves are diverse and include snowshoe hares (Lepus americanus) and beavers (Castor canadensis).

I estimated kill rate, prey selection, and prey availability for 4 wolf packs for 30-day periods March 1989, March 1990, and November 1990. I calculated predation rates (mortality rates due to wolf predation) by dividing estimates of kill rate by their respective caribou density estimates. Detailed methods for estimating kill rate are presented in Chapter 1. I then used SPSSx, and BMDP nonlinear regression programs to fit equations to observed and theoretical numerical and functional responses. Where possible and appropriate, I used theoretical equations from the literature.

My model consists simply of a functional response (wolf kill rate) and a numerical response (number of wolves) to estimate the proportion of the caribou population killed over a range of prey densities on a daily basis. Because functional response was only measured in early and late winter over a period of two years, the model assumes that the shape of the functional response curve does not change over time, either within or among years.

I used the Type II functional response described by Holling (1966):

$$[1]\ N_a = aNT \div (1 + at_hN)$$

where N_a is the kill rate (caribou killed/wolf/day), N is the caribou density (caribou/km^2), and a and t_h are constants representing efficiency and handling time. I used the simple logistic equation to generate a Type III (sigmoidal) response:

$$[2]\ N_a = aT \div (1 + b^{-c}N)$$

where the constants a, b, and c do not have any specific biological meaning, but determine the shape of the curve.

The numerical response I used was the linear relationship between the biomass of all ungulate prey and wolf density (Keith 1983, Fuller 1989). Because this numerical relationship is derived from some populations that have stabilized, it may not reflect the actual numerical responses of wolves to changes in prey abundance. Nonetheless, wolf population trends are often thought to lag prey population trends (Peterson and Page 1983, Theberge and

Gauthier 1985, Theberge 1990), and lags generally have an anti-regulatory (i.e., destabilizing) influence on population dynamics (Lidicker 1978).

Time lags in numerical response were incorporated into the model by assuming that changes in the caribou population size averaged 5% when they occurred. Thus a 1-year time lag for an increasing prey population was estimated by calculating the number of wolves predicted by 95% of the actual prey population. Likewise a 2-year lag would use a wolf estimate based on 90% of the actual prey population. I tested time lags from 0-10 years (Peterson et al. 1984). There was no need to simulate variation in the magnitude of yearly population change in the caribou population, because in the model a 10% change in one year would have the same effect as a 2-year lag with a 5% change. The output of the model is the total response (proportion of the caribou population killed by wolves/day), similar to the Predation Index presented by Messier (1991).

RESULTS

The observed functional response

Eleven estimates of prey selection, kill rate, and prey availability were obtained, 4 in March 1989, 4 in March 1990, and 3 in November 1990. Prey switching related to caribou abundance was not observed (Table 1). Analysis of the observed functional response indicated no regions of increasing slope (Fig. 3). Therefore, Holling's disc equation adequately fit my data (Fig. 4) and the functional response was judged to be type II. When incorporated into the model, the estimated effect of wolf predation was highly destabilizing, characterized by high predation rates at low densities, and low predation rates at high densities (Fig. 5). Time lags in the numerical response exacerbated the destabilizing effect of wolf predation for decreasing populations, and moderated the destabilizing effect for increasing populations.

Evaluating a sigmoidal (type III) functional response

I constructed a hypothetical curve to evaluate the effects of wolf functional response that is sigmoidal due to changes in caribou vulnerability. I used the maximum kill rate from the observed data and placed the inflection point of the curve at the total prey density where caribou and moose were equally abundant. This functional response, in conjunction with the linear numerical response, produced a

Table 1. Caribou density, prey selection, and kill rate estimates for wolves in Gates of the Arctic National Park, Alaska, USA.

Pack	Traveling Pack Size	Caribou/km^2	Percentage of Caribou in kill	Caribou/ wolf/day
March 1989				
Walker L.	6.1	2.34	85	0.10
Iiniakuk	4.8	0.31	86	0.10
Unakerak	7.7	0.08	93	0.07
Sixty Mi.	8.5	0.07	100	0.06
March 1990				
Walker L.	9.8	1.19	100	0.09
Iniakuk	4.4	0.19	100	0.10
Unakserak	6.0	0.21	92	0.11
Pingaluk	6.1	0.50	100	0.08
November 1990				
Iniakuk	5.4	0.06	100	0.10
Unakserak	12.2	0.41	96	0.11
Pingaluk	10.6	0.24	64	0.03

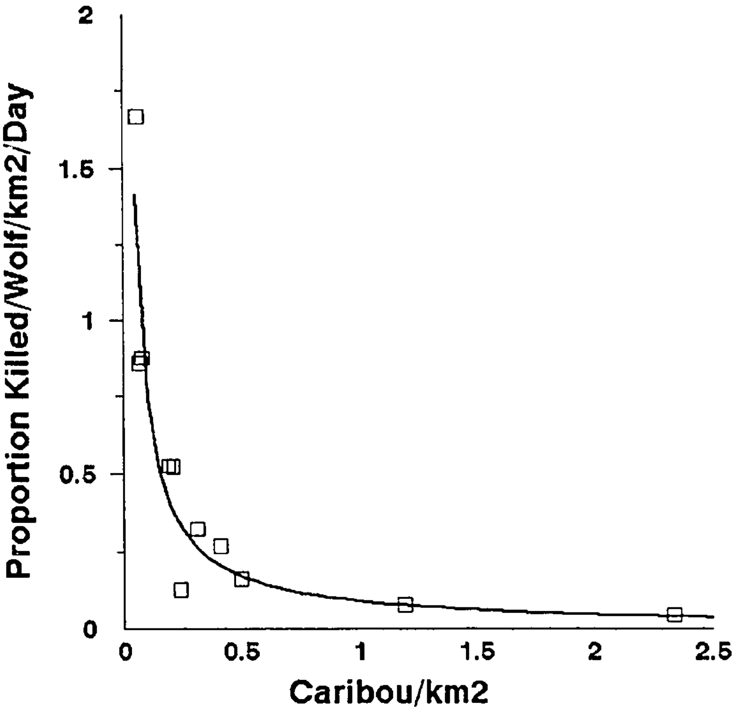

Fig. 3. Observed winter predation rate estimates on caribou for wolves in Gates of the Arctic National Park, 1989-90 ($\underline{r}^2$=0.89, $\hat{Y}=0.09*X^{-0.92}$).

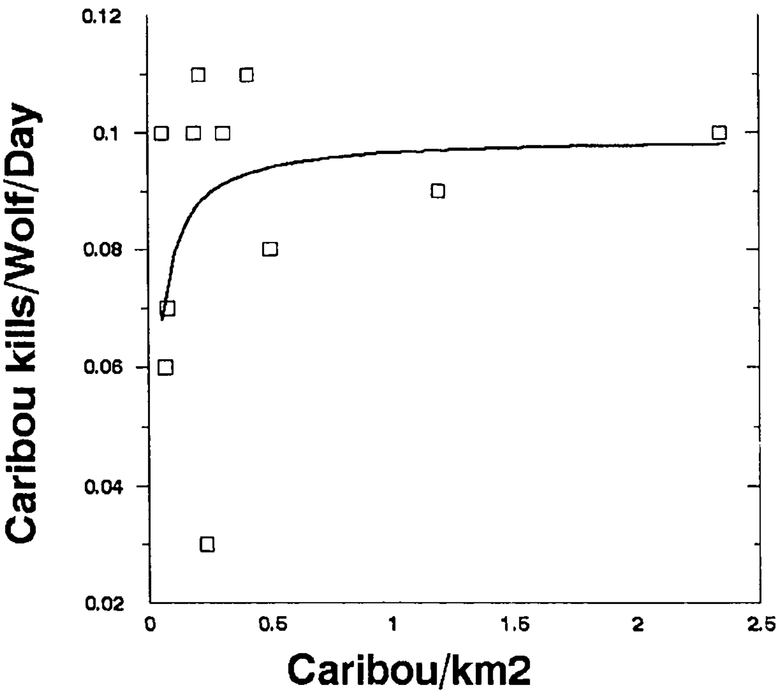

Fig. 4. Observed winter kill rate estimates fitted by Holling's (1965) disc equation ($\underline{r}^2$=0.80, the assumption that kill rate=0 at 0 caribou/km^2 was necessary to fit Eq [1]).

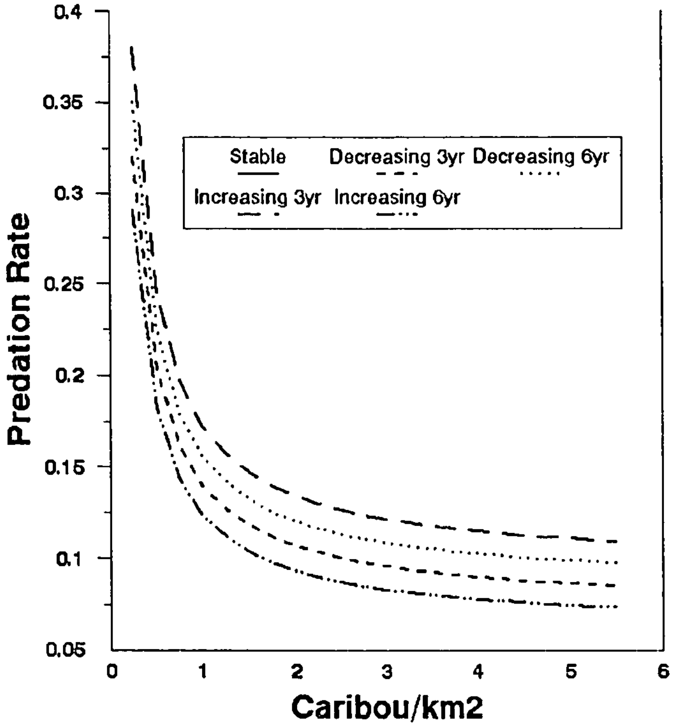

Fig. 5. Total response (functional response * numerical response) of wolves to varying caribou abundance modeled with the observed type II functional response. Lags in numerical responses are based on 5% changes in caribou abundance per year.

region of stability at low caribou densities (Fig. 6). Time lags moderately washed out the region of stability for increasing populations.

DISCUSSION

Functional response

I predicted that the functional response of wolves to variation in caribou abundance would be sigmoidal in Gates of the Arctic National Park due to changes in prey selection that would result in increasing specialization on caribou as caribou density increased. Because the observed functional response was type II, I reject that hypothesis. Indeed, the observed functional response describes an extremely efficient predator specializing on caribou even at low densities. In addition, I can reject the hypothesis that bioenergetic optimization of search time resulted in a sigmoidal functional response under the observed conditions.

As noted previously, a sigmoidal functional response also may be caused by density-dependent changes in prey vulnerability (Holling 1966, Wood and Hand 1984). I can, however, only speculate on the influence of density-dependent changes in caribou vulnerability on the shape of the functional response curve because the treatments in this experiment consisted of caribou from a single herd. Whether density-dependent competition for food in low-density prey

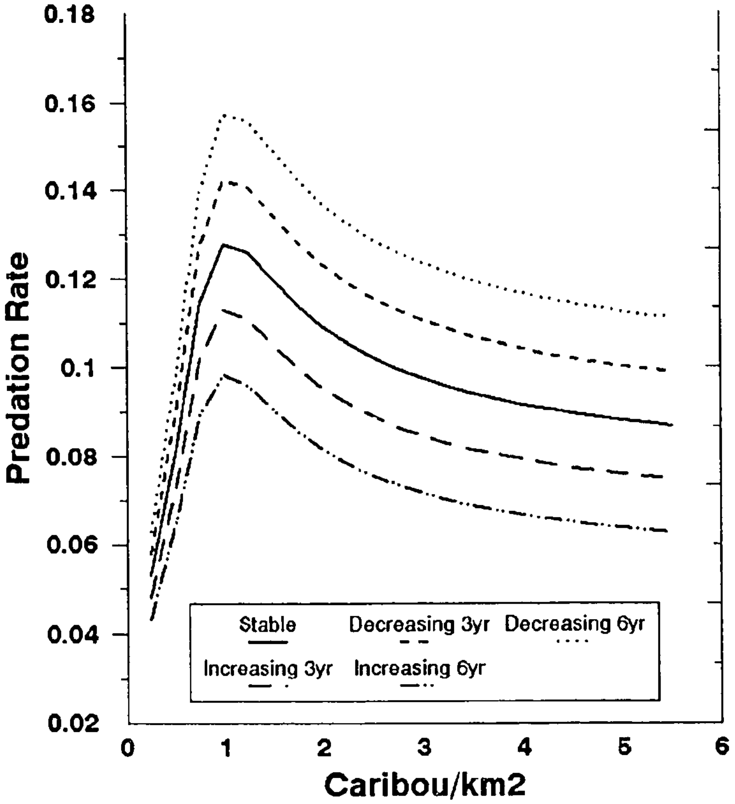

Fig. 6. Total response (functional response * numerical response) of wolves to varying caribou abundance modeled with a hypothetical type III functional response. Lags in numerical responses are based on 5% changes in caribou abundance per year.

populations results in changes in vulnerability to wolf predation is unknown, but seems unlikely. Even so, significant changes in vulnerability may simply result in a change in the intercept of the observed response, and not change the shape of the curve.

Functional response has not been estimated for large mammalian predators, but studies of invertebrates (Akre and Johnson 1979) suggest that predators that can switch to alternate prey are more likely to produce sigmoidal functional responses. Nonetheless, when predators are at or near food satiation, optimal foraging behavior would predict decreasing predation effort with increasing prey density even with switching (Sih 1984). Wolves in open, multiple-ungulate prey systems often may be near food satiation because extremes in food availability result in numerical responses through immigration, timing and rates of dispersal, and rates of survival (Zimen 1976, Packard and Mech 1980, Page 1989, Dale et al. 1992). When one ungulate prey species is preferred, wolves are likely to have a destabilizing functional response for that prey species (Oaten and Murdoch 1975b).

Haber (1977) and Walters et al. (1981) estimated kill rate and prey availability for wolves in Denali National Park, Alaska. In that study, data were fit to Charnov's (1973) multi-species disc equation, an extension of equation

[1]. This equation assumes a type II functional response. In their model for the Denali moose herd, however, Haber and Walters included a switch from moose calves to caribou when moose numbered <100 in a pack territory. This component of the model allowed the moose herd to grow and provided the lower of the 2 stable equilibria proposed by the model. The Haber and Walters model illustrated how prey switching might result in regulation of prey despite a type II functional response (Fig. 7). This switching was not observed in GAAR, however, as caribou were the primary prey even when moose were more abundant.

Regulation of barren-ground caribou

My model, although based on empirical data, is limited in scope. These data do indicate that wolf predation can be an important limiting factor at low caribou densities, and may have an anti-regulatory effect. Further, the model provides some insight into the likelihood and conditions under which regulation of barren-ground caribou in multi-prey systems might occur. Based on the shape of the observed functional response, I reject the hypothesis that there is a behavioral mechanism resulting in regulation of caribou at a low-density equilibrium or at some high-density equilibrium.

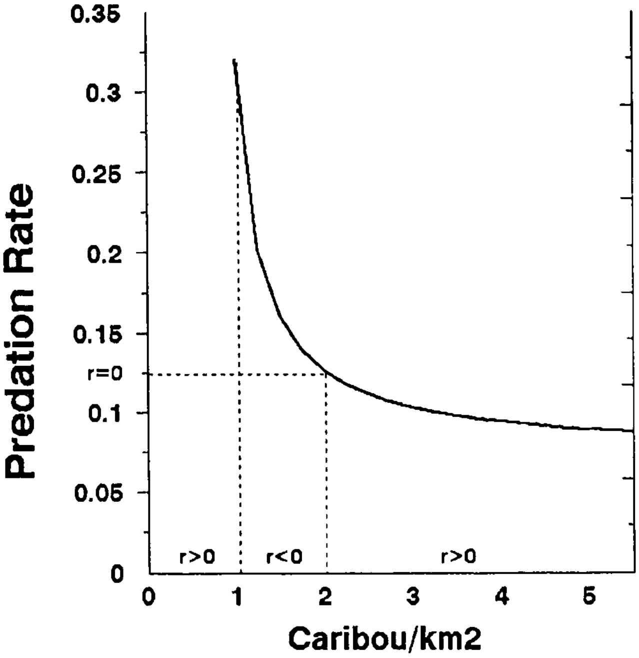

Fig. 7. Hypothetical model illustrating a potential stable equilibrium generated by prey switching despite a type II functional response. The stable region (around 1 caribou/km^2) occurs when the intrinsic growth rate of the population (r) happens to equal 0 near the asymptote of the total predation response curve.

Either a less efficient (flatter) Type II, a Type III functional response or a different numerical response is requisite for either outcome.

There was no region of positive slope generated by the "multiplicative effect" of increasing functional and numerical responses (Seip 1991) because the narrow region of positive slope in kill rate was negated by a decreasing wolf:caribou ratio caused by the rather large positive constant in the equation for the numerical response. Obviously, assumptions about intercepts, and the accuracy of data that influences solutions for constants have tremendous influences on the outcome of these models.

Numerical response of predators to changes in prey density has been indicated as a mechanism for prey population regulation in small mammals (Sinclair et al. 1990). Bergerud (1980) and Messier and Crete (1985) suggested that, for wolves, the very high growth potential of a population consisting of fragmented packs, singles, and pairs may result in regulation of caribou and moose populations. In this scenario, the wolf population responds to shifts in prey abundance by collapsing to pairs or becoming re-established as packs depending on the direction of the shift. In other words, the equation describing the numerical response has a negative constant. It is unlikely that numerical responses would result in regulation of caribou herds that live in multiple-ungulate prey systems because the wolf population would not collapse as is more likely to occur in a single prey system (Messier 1985, Messier and Crete 1985, Theberge and Gauthier 1985). In addition the constant in the equation for the numerical response will be significantly positive because a viable wolf population is supported by alternate ungulate prey. Furthermore, wolves in single-prey systems do not necessarily respond as proposed (Mech 1977, 1986, Peterson 1977).

Most of the many components of real systems not represented in the model are destabilizing. Stochastic variation in the nutrient-climate ceiling is destabilizing because predator:prey ratios and vulnerability of prey can change drastically. Although it may be argued that the magnitude of the effect of limiting weather events is density-dependent (Picton 1984), the concurrent effects of predation can make them destabilizing. Bear predation is thought to be density-independent or inversely density-dependent (Ballard and Larsen 1987, Ballard and Miller 1990, Ballard 1991, 1992). When 2 or more predators have destabilizing functional responses, the efficacy of predator reduction or other attempts to increase ungulate abundance (Beortje et al. 1992) may be enhanced (Fig. 8). A reduction in the impact of one predator results in a small increase in

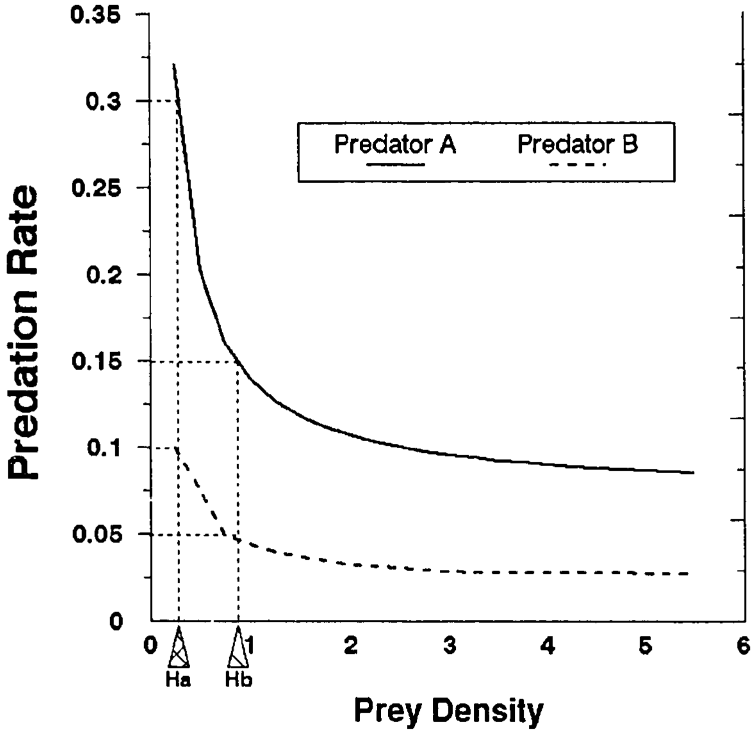

Fig. 8. Synergistic effect of a reduction in the magnitude of predation from one predator when 2 or more predators have destabilizing total responses to changes in prey density. Reducing the predation rate of predator B from 0.1 to 0.05, allows the population to increase slightly from Ha to Hb. At Hb, the predation rate due to predator B declines to about 0.15. The total predation rate (predator A + predator B) is reduced from 0.35%/day to 0.2%/day.

the prey population. At the higher prey density, the impact of the second predator is reduced due to the inversely density-dependent relationship. This may explain why wolf reductions have been successful in areas where bear predation is the dominant limiting factor (Ballard 1991).

The often clumped spatial distribution of caribou is destabilizing because of the swamping effects of high densities (Bergerud 1974, Cumming 1975). If caribou became more evenly distributed as the herd grew to the point where densities within wolf-pack territories actually decreased, wolf predation could have a stabilizing effect because more packs of wolves would be preying on the population. Nevertheless, ecological density of barren ground caribou apparently increases with herd growth (Messier et al. 1988). In view of this effect of spatial distribution, my model represents predation rate as a function of the density at which the average caribou in the population lives throughout the year. A clumped spatial distribution exacerbates the destabilizing shape of the predation response curve from this average, whereas use of seasonal ranges shifts the curve along the ordinate axis because of a reduced numerical response of wolves to seasonal prey availability.

The obvious exception to these factors destabilizing prey populations is competition for food, or other resources, which has a regulatory effect at high population densities (Klein 1968, Messier et al. 1988, Messier 1991). The feedback for this regulation may not be immediate enough to cause a stable equilibrium in the case of caribou (May 1981, Peterson et al. 1984).

Investigation of limiting, stabilizing, and regulating factors is fundamental to understanding wolf-prey dynamics. The results of this analysis support the theory that predators, such as wolves, can have an anti-regulatory effect on prey populations (Lidicker 1978, Potvin et al. 1988, Theberge 1990, Ballard 1991, Messier 1991). Nonetheless, further knowledge of the factors affecting prey switching, and additional descriptions of functional and numerical responses are needed to draw firm conclusions.

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