Kill rate by wolves on moose in the Yukon

R.D. Hayes, A.M. Baer, U. Wotschikowsky, and A.S. Harestad

Abstract: We studied the kill rate by wolves (*Canis lupus*) after a large-scale wolf removal when populations of wolves, moose (*Alces alces*), and woodland caribou (*Rangifer tarandus caribou*) were all increasing. We followed a total of 21 wolf packs for 4 winters, measuring prey selection, kill rates, and ecological factors that could influence killing behavior. Wolf predation was found to be mainly additive on both moose and caribou populations. Kill rates by individual wolves were inversely related to pack size and unrelated to prey density or snow depth. Scavenging by ravens decreased the amount of prey biomass available for wolves to consume, especially for wolves in smaller packs. The kill rate by wolves on moose calves was not related to the number of calves available each winter. Wolves did not show a strong switching response away from moose as the ratio of caribou to moose increased in winter. The predation rate by wolves on moose was best modeled by the number and size of packs wolves were organized into each winter.

Résumé : Nous avons étudié la prédation par le Loup gris (*Canis lupus*) dans un système d'où une proportion importante des loups ont été retirés à un moment où les populations de loups, d'Orignaux (*Alces alces)* et de Caribous des bois (*Rangifer tarandus caribou*) étaient en plein essor. Nous avons suivi 21 meutes de loups pendant quatre hivers au cours desquels nous avons mesuré la sélection des proies, la proportion de proies tuées et les facteurs écologiques qui peuvent influencer le comportement d'attaque mortelle. La prédation par les loups s'est avérée additive au sein des populations d'orignaux et de caribou. Les taux d'attaques mortelles par des individus étaient fonction inverse de la taille de la meute et indépendants de la densité des proies ou de l'épaisseur de la neige. Le comportement détritivore du Grand Corbeau *(Corvus corax)* a eu pour effet de diminuer la quantité de viande d'ongulé que pouvaient consommer les loups, particulièrement au sein des meutes plus petites. Le taux d'attaques mortelles de jeunes orignaux par les loups n'était pas relié au nombre de jeunes orignaux disponibles chaque hiver. Les loups n'ont pas transféré leurs efforts de prédation vers d'autres proies lorsque le rapport caribous : orignaux a augmenté en hiver. Les taux de prédation exercée par les loups sur les orignaux correspondent particulièrement bien au modèle basé sur le nombre et la taille des meutes que forment les loups chaque hiver.

[Traduit par la Rédaction]

Introduction

Predation by wolves (*Canis lupus*) is a primary force limiting moose (*Alces alces*) (Peterson 1977; Gasaway et al. 1983, 1992; Peterson et al. 1984; Ballard et al. 1987; Ballard and Van Ballenberghe 1997) and woodland caribou (*Rangifer tarandus caribou*) populations (Gasaway et al. 1983; Gauthier and Theberge 1985; Edmonds 1988; Seip 1991*a*, 1992). Determining how wolves behave in relation to changing availability of prey can provide insight into the nature of their functional response (Theberge 1990; Messier 1991, 1994; Seip 1991*b*; Dale et al. 1994; Hayes and Harestad 2000*b*). To best understand the functional response, kill rates by wolves need to be measured across a range of prey densities, while controlling for other ecological variants that could influence kill rates (Boutin 1992).

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The supply of prey to predators depends upon both the number of prey individuals and their vulnerability to being killed (Solomon 1949). Vulnerability of ungulates to predation by wolves depends upon (*i*) prey density (Messier and Crête 1985; Messier 1991, 1994); (*ii*) age, size, and physical condition of prey (Peterson and Page 1983; Ballard et al. 1987); (*iii*) availability of alternative prey (Peterson and Page 1983); (*iv*) low plasticity of wolves to prey switch (Mech and Karns 1977); and (*v*) snow depth (Peterson 1977; Huggard 1993; Mech et al. 1998). The kill rate has been related to wolf-pack size (Hayes et al. 1991; Thurber and Peterson 1993).

We describe wolf-predation behavior during a period when wolf, moose, and caribou were all increasing. We examine whether predation in winter was additive or compensatory mortality for ungulates. We also examine the influence of wolf density, wolf-pack size, moose density, availability of caribou prey, small-mammal abundance, and snow depth on prey selection and kill rate by wolves. We estimate the proportion of moose killed by wolves in winter and assess the importance of wolf predation on survival of adult and calf moose.

We tested 4 hypotheses concerning predation by wolves:

$H_0 1$: Wolf predation is additive mortality on prey populations;

$H_0 2$: The kill rate by wolves is dependent on prey density; $H_a 2$: The kill rate by wolves is independent of prey density and related to wolf-pack size;

$H_0$3: The kill rate by wolves on moose calves depends on the proportion of calves alive in winter;

$H_0$4: The kill rate by wolves on moose decreases when the availability of caribou exceeds that of moose.

Methods

We studied wolf kill rates in winter in the 23 000-km^2 Finlayson Lake Study Area (FSA) in the east-central Yukon (62°N, 128°W) from February 1990 through March 1994. Hayes and Harestad (2000a) describe the study area. Wolves were reduced in the area during the 1980s (R. Farnell, Yukon Fish and Wildlife Branch, Box 2703, Whitehorse, YT Y1A 2C6, Canada, unpublished data), and the wolf population increased rapidly during our study (Hayes and Harestad 2000a).

Other biologists estimated moose abundance in two regions in the FSA before (Jingfors 1988) and during our study (Larsen and Ward 1995). In the North Canol area, moose annually increased at a finite rate of 1.16 from November 1987 to 1991, for a density of 339 ± 61 (mean ± 90% confidence interval (CI)) moose/1000 km^2 (Larsen and Ward 1995). Similarly, in the Frances Lake area, moose increased at a finite rate of 1.18, for a density of 381 ± 80 (mean ± 90% CI) moose/1000 km^2 in winter 1992 (Larsen and Ward 1995). We calculated the mean moose density for the two areas in winter 1990 and 1991 by interpolating between these surveys, assuming a constant rate of increase (Appendix, Table A1). We extrapolated the rate of increase between 1992 and 1993 from Larsen and Ward (1995). From 1993 to 1994, we projected population change on the basis of adult mortality and calf recruitment rates, after the formula of Hatter and Bergerud (1991): $\lambda = (1 - M)/(1 - R)$, where M is adult mortality rate and R is the proportion of moose calves observed in March 1994 (Appendix, Table A1). We estimated that overall moose density in the FSA increased from 263/1000 km^2 in 1990 to 443/1000 km^2 in 1994 (Appendix, Table A1). After 1994, moose-calf survival rates and moose density apparently declined in the area. In 1996, R. Ward (Yukon Fish and Wildlife Branch, Box 2703, Whitehorse, YT Y1A 2C6, Canada, unpublished data) estimated moose densities of 278 ± 53/1000 km^2 (mean ± 90% CI) in the North Canol area and 337 ± 71/1000 km^2 (mean ± 90% CI) in the Frances Lake area. Densities were not significantly different from 1991 estimates, but apparently declined from our projected estimate in 1994 (Appendix, Table A1).

Caribou were counted using stratified random block surveys in 1987 (Farnell and MacDonald 1988), 1991 and 1996 (R. Farnell, unpublished data). The herd increased at a mean finite rate of 1.18, growing to 5950 ± 18% (mean ± 90% CI) animals in winter 1991 (R. Farnell, unpublished data). After 1991, herd growth slowed and possibly declined by 1996 as recruitment dropped. Herd size in 1996 was 4536 ± 12% (mean ± 90% CI) animals, but was adjusted to about 5000 because of bulls missing from surveys.

Hayes and Harestad (2000a) describe methods for estimating wolf density and radiotelemetry techniques. We defined the kill rate as the number of moose killed per day by each wolf (to study moose population dynamics) or the total biomass (kg) of ungulate prey killed per day by each wolf (to study wolves' consumption rates). The daily area traveled by each pack was estimated from 100% area convex polygons (Ackerman et al. 1990).

We estimated kill rates by locating packs of radio-collared wolves at regular intervals during February and March of 1990 and 1992 and during March of 1991 and 1994. We defined each series of consecutive daily or bi-daily relocations as a predation period. We defined wolf-pack size as the mean number of wolves seen during each predation period (Messier 1994; Dale et al. 1995). Aircraft crews observed wolf behavior using methods of Mech (1974). When observers located a radio signal, they counted wolves and searched the area for ungulate carcasses. If most pack members were not seen, aircraft crews followed wolf trails to find missed in-

dividuals and locate any kills. From the air we classified all dead moose as calf or non-calf (yearling and adult combined) according to differences in size and body shape (Peterson 1977).

The interval between locations varied according to the composition of ungulate species in pack territories. Wolves usually spend more than 48 h handling a moose carcass (Peterson et al. 1984; Messier and Crête 1985; Ballard et al. 1987; Hayes et al. 1991). Therefore, we located a pack every 24–48 h if only moose prey were available and twice each day, usually between 9:00 and 11:00 and between 16:00 and 19:00, if caribou were also available. We compared kill rates with location intervals to test for any temporal bias. If a pack was not seen for more than 3 consecutive days, we ended the observation because a moose could be killed and consumed within that period (Peterson et al. 1984; Hayes et al. 1991).

We divided causes of ungulate mortality into wolf predation, and other natural and human causes. We assumed that wolves killed an animal when there was fresh blood spoor, or when snow trails showed that the animal had been recently attacked by wolves. We assumed that wolves were scavenging if a carcass was found lying on its sternum (Stephenson and Sexton 1974; Ballard et al. 1987; Hayes et al. 1991) or there were signs that other animals had fed on the carcass before wolves did. Human causes included killing by hunters or trappers or being hit by a vehicle.

We visited a sample of in situ prey carcasses each winter to determine their sex, age, and physical condition. Moose sex was determined from antler pedicels and ileum morphology and caribou sex from the size and shape of antlers. We collected incisor bars from killed moose to determine age (Sergent and Pimlott 1959). We also collected long bones from killed moose and caribou to assess nutritional condition (Neiland 1970). We kept bones frozen to minimize dehydration loss (Peterson et al. 1982). Even when moose carcasses were mostly consumed, many could still be classified as either calf or adult from the size and shape of moose fecal pellets on site.

We estimated the live mass of adult female moose in late winter at 375 kg (Franzmann et al. 1978) and adult bulls at 413 kg (Schwartz et al. 1987). We assigned a mass of 400 kg to animals of unknown sex, 250 kg to yearlings, 150 kg to calves (Ballard et al. 1987), 152 kg to adult caribou (R. Florkiewicz, Yukon Fish and Wildlife Branch, Box 2703, Whitehorse, YT Y1A 2C6, Canada, unpublished data), 55 kg to calf caribou (Skoog 1968), and 75 kg to Dall sheep (*Ovis dalli dalli*) (Sumanik 1987; Hayes et al. 1991).

Consumable biomass of caribou was 75% of live mass (Ballard et al. 1987). We estimated that consumable biomass of moose was 65% after weighing 7 moose carcasses on the day that wolf packs abandoned them. Ravens (*Corvus corax*) were important scavengers in our study area during winter (Promberger 1992). We used data from Promberger (1992) to adjust wolf consumption to account for raven scavenging, depending on wolf-pack size.

We defined the predation rate as the proportion of prey that were killed daily (Messier 1994). We estimated the winter predation rate by multiplying daily kill rates by 182 days, then dividing by the mean moose density.

Annual snow data were collected in early March at 7 stations in our study area (G. Ford, Government of Canada Water Resources, Whitehorse, Yukon, unpublished data). We compared kill rates with March snow depth obtained from the station nearest each pack's territory. We used linear regression analysis to examine relations between kill rate and several independent variables.

Results

Types of ungulates killed by wolves

During all winters we found 326 ungulate carcasses, including 291 moose (89%), 30 caribou, 1 Dall sheep, and 4 unidentifiable kills. We determined that 286 moose were killed by wolves (Table 1). We visited 51 kills in situ. During

Table 1. Proportions of moose calves killed by wolves and in late winter composition counts.

Year	Wolf-killed moose		Moose in March population		$H_0: P_k = P_p$	
	No.	Proportion of calves (P_k)	No.	Proportion of calves (P_p)	χ^2	P
1990	55	0.55	156	0.36	13.8	<0.01
1991	16	0.25	265	0.37	1.0	<0.01
1992	135	0.26	215	0.26	1.2	0.28
1993	33	0.12	101	0.22	0.6	0.44
1994	47	0.32	332	0.11	14.3	<0.01

Note: The χ^2 values show the differences between the proportion of calves in the kill sample (observed) and the proportion of live calves in winter (expected). Yates' corrected χ^2 was used for 1991 and 1993 because of small sample sizes of calves in the kill sample.

predation-rate study periods we found 179 of the moose kills and 25 caribou kills (Appendix, Table A2).

Wolves preyed on moose calves more often than on other age-classes. Calves accounted for 31% ($n = 88$) of killed moose (Table 1). We found no consistent relation between the proportion of calves in the wolves' diet and the proportion of calves available each winter (Table 1).

The age of 27 killed adult moose that were aged was 8.9 ± 0.9 (mean ± SE) years, ranging from 2 to 15 years (Fig. 1). Wolves killed 28 female and 18 male moose (>1 year old). Mean age did not differ between the sexes. We found 30 caribou carcasses but we could not distinguish sex or age from aircraft. Large wolf packs completely consumed caribou in a few hours, leaving few remains for identification.

Nearly all killed prey were apparently not in starving condition at the time of death. Starvation levels are <10% marrow fat for moose calves and <20% for adults (Peterson et al. 1984). Marrow fat content of wolf-killed calves ($n = 23$) was 34 ± 4% (mean ± SE; range 11–78%) and that of adults ($n = 26$) was 77 ± 3% (mean ± SE; range 52–95%) (Fig. 2). No moose were within starvation range, but 35% of calves were close. Seven adult caribou had 66 ± 14% (mean ± SE) marrow fat (range 8–95%).

Kill and consumption rates by wolves

We studied kill rates in 21 different wolf packs during 4 winters (Appendix, Table A2). Traveling pack size ranged from 2 to 20 wolves. The predation period was 20 ± 1.3 (mean ± SE) days, ranging from 6 to 39 days (Appendix, Table A1). We measured kill rates of small packs (2 or 3 wolves) during 18 predation periods, medium packs (4–9 wolves) during 13 periods, and large packs (≥10 wolves) during 14 periods. In total, we sampled kill rates of 283 wolves during 6153 wolf-days (982 pack-days). We observed packs for 71 ± 0.9% (mean ± SE) of all days during predation periods (Appendix, Table A2).

Moose composed 94% (57 764 kg) of the biomass of ungulates killed. The kill rates were 0.045 ± 0.004 (mean ± SE; range 0.013–0.123) moose/day by each wolf and 0.193 ± 0.085 moose/day by each pack. Other studies showed that pack size strongly affected kill rates (Hayes et al. 1991; Thurber and Peterson 1993; Dale et al. 1994). The log-transformed model $y = \log_{10}$ of pack size minimized heteroscedasticity for both kilograms (mass) of prey killed per wolf

Fig. 1. Frequencies of moose in age-classes older than calves that were killed by wolves during winter in the study area.
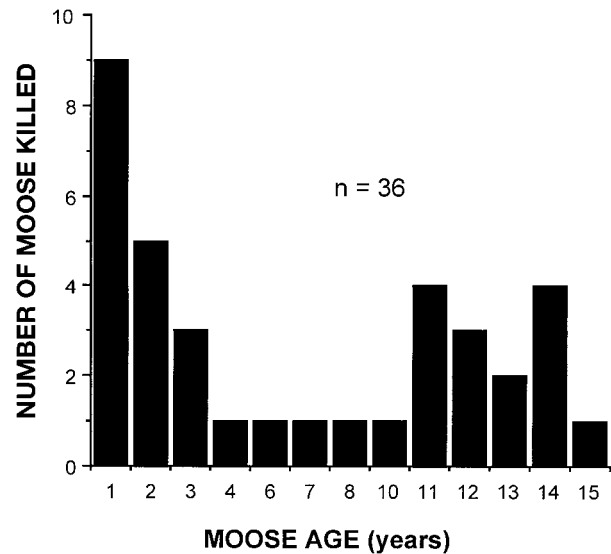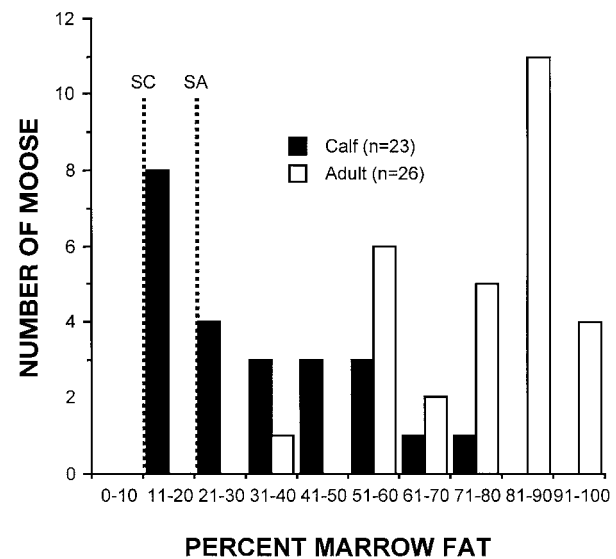

Fig. 2. Marrow-fat indices (%) for adult and calf moose killed by wolves during winter. "SA" is starvation level for adult moose and "SC" is starvation level for calf moose (Gasaway et al. 1992).

each day (KGWD) and the number of moose killed per wolf each day (MWD). $\log_{10} y$ = pack size was the best linear model for the period between moose kills (days per moose kill, DMK). Thurber and Peterson (1993) used the same log-transformed models in a similar analysis of wolf kill rates.

Because we measured kill rates of some packs more than once, we examined the data for dependence problems. We examined a regression equation for KGWD and $\log_{10}$ pack size using data from the last (or only) predation period for the 21 different packs studied ($y = -17.4 - 5.35 \log_{10}$ pack size). Parameters differed little from the equation for the pooled predation data ($y = -16.8 - 5.4 \log_{10}$ pack size). Thus, we used the pooled rates in our regression analyses. We also tested for any relation between kill rate and intervals between relocations, expressed as the percentage of days on

Table 2. Results of linear regression analysis of kill rates by wolves on ungulates (kg/wolf/day), moose (moose/wolf/day), and killing intervals on moose ($\log_{10}$ days/moose kill) and moose calves ($\log_{10}$ days/calf kill) with various independent variables.

Dependent variable	Independent variable	r^2	df	P
kg/wolf/day	km²/day	0.01	44	0.49
	Moose density	0.03	44	0.28
	Moose/wolf	0.002	44	0.78
	Number of packs	0.001	44	0.97
	Percentage of days seen	0.03	44	0.28
	$\log_{10}$ pack size	0.40	44	**<0.001**
Moose/wolf/day	$\log_{10}$ pack size	0.57	43	**<0.001**
$\log_{10}$ days/kill	km²/day	0.001	43	0.87
	Moose density	0.02	43	0.93
	Moose/wolf	0.006	43	0.98
	Percentage of days seen	0.10	43	0.52
	Snow depth	0.003	41	0.75
	Pack size	0.37	43	**<0.001**
$\log_{10}$ days/calf kill	Moose density	0.001	31	0.90
	Percentage of moose calves alive in late winter	0.001	31	0.84
	Pack size	0.004	44	0.74
	Snow depth	0.008	41	0.58

Note: Values in boldface type indicate that the independent variable is significantly related.

Fig. 3. Kill rates during winter by wolf packs of different sizes in the FSA ($\log_{10} y = 0.93 - 0.03x$).
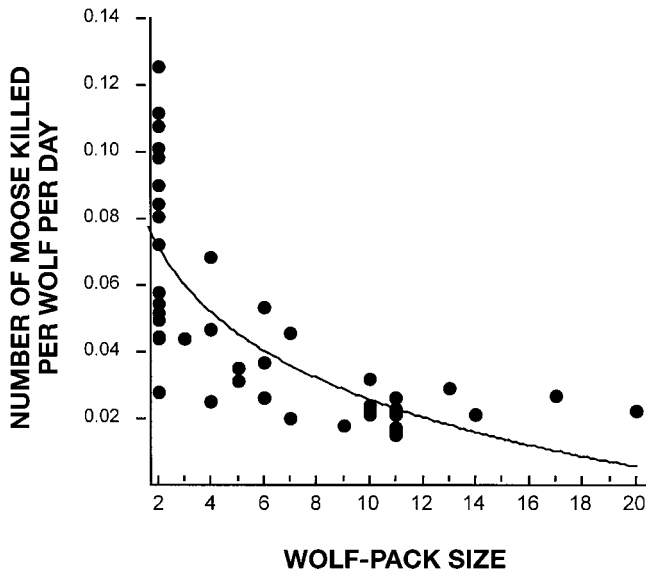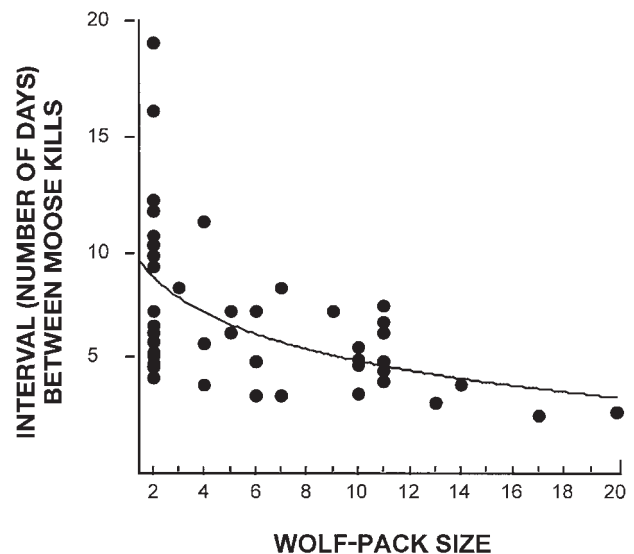

Fig. 4. Intervals between moose kills during winter for wolf packs of different sizes in the FSA ($\log_{10} y = 0.93 - 0.03x$).

which wolves were seen. We found no correlation (Table 2), indicating that we sampled daily activities often enough to find most kills.

Kill rate was significantly correlated only with wolf-pack size (Table 2). It was not related to (*i*) daily area (km²) in which wolf packs traveled, (*ii*) percentage of days on which wolves were followed, (*iii*) annual ratio of wolf numbers to moose numbers, (*iv*) number of wolf packs, (*v*) snow depth, or (*vi*) moose density (Table 2). The kill rate by wolves on moose calves ($\log_{10}$ days/calf kill) was not related to any variable, including the proportion of calves alive in winter (Table 2).

Both KGWD ($r^2 = 0.40$, df = 44, $P < 0.001$) and MWD (Fig. 3; $r^2 = 0.57$, df = 43, $P < 0.001$) were inversely related to $\log_{10}$ pack size. Log_{10} DMK was inversely related to wolf-pack size (Fig. 4; $r^2 = 0.37$, df = 43. $P < 0.001$). We excluded small packs to test whether kill rates remained significantly correlated with the sizes of larger packs (4–20 wolves). KGWD remained inversely related to $\log_{10}$ pack size ($r^2 = 0.37$, df = 26, $P = 0.001$). Excluding small packs did not improve the relation between $\log_{10}$ DMK and moose density ($r^2 = 0.007$, df = 25, $P = 0.69$). Excluding wolf pairs did improve the relation between $\log_{10}$ days/calf kill and the ratio of numbers of live calves to numbers of adult moose ($r^2 = 0.11$, df = 24, $P = 0.11$), but it was not significant.

Table 3. Proportions of all moose and of non-calf moose killed by wolves each winter, 1990 through 1994.

Winter	Total no. of moose[a]	No. killed[b]	% of total killed	Total no. of non-calves[c]	No. of non-calves killed[d]	% of non-calves killed
1990	4537	436	0.10	2904	196	0.07
1991	5313	736	0.14	3347	552	0.16
1992	6227	912	0.15	4608	675	0.15
1993	6952	991	0.14	5422	872	0.16
1994	7642	1037	0.14	6801	705	0.10

[a]Based on mean moose density (Appendix, Table A1), a total area of 23 000 km^2, and 75% habitable moose range (our calculations).
[b]Based on the pack kill rate for the winter period.
[c]From Table 1 (proportion of non-calf moose seen in March obtained by subtraction).
[d]From Table 1 (proportion of non-calf moose killed by wolves obtained by subtraction).

There was no correlation between the daily area (km^2) in which wolves traveled (i.e., prey-searching rate) and $\log_{10}$ pack size ($r^2 = 0.02$, df = 44, $P = 0.33$). Small packs traveled 23 ± 5 (mean ± SE), medium packs 18 ± 5, and large packs 28 ± 4 km^2/day. Daily area of travel was unrelated to either moose density ($r^2 = 0.04$, df = 44, $P = 0.18$) or the ratio of moose numbers to wolf numbers ($r^2 = 0.04$, df = 44, $P = 0.17$). These nonsignificant relations indicate that competition for prey resources did not influence prey-searching rates of wolves.

We found no difference in the handling times (number of days packs spent on kills) between adult moose ($n = 65$, 2.9 ± 0.17 (mean ± SE) days) and calf-moose kills ($n = 35$, 2.6 ± 0.22 days). Handling times for adult moose did not differ (Kruskal–Wallis test, $\chi^2 = 5.4$, $n = 65$, $P = 0.07$) between small ($n = 17$ kills, 3.3 ± 0.19 days), medium ($n = 19$, 3.1 ± 0.5 days), and large packs ($n = 29$ kills, 2.6 ± 0.16 days).

Handling time for moose calves differed with pack size (analysis of variance (ANOVA), $F_{[37]} = 3.9$, $P = 0.03$). Small packs averaged 3.3 ± 0.3 (mean ± SE) days ($n = 16$ kills), medium packs averaged 2.5 ± 0.3 days ($n = 8$ kills), and large packs averaged 2.0 ± 0.3 days ($n = 29$). Caribou kills ($n = 13$) were handled for an average of 1.3 ± 0.1 days. We saw some large packs consume caribou in a few hours, making it difficult to accurately estimate caribou handling times.

Large numbers of wintering caribou were available to 4 packs during 11 predation periods. Although caribou greatly outnumbered moose, packs still killed more moose ($n = 40$) than caribou ($n = 20$). Biomass of the moose killed by each of these wolves per day was 7.9 ± 0.7 (mean ± SE) kg compared with 2.5 ± 0.6 kg of caribou.

Snowshoe hare availability did not influence the kill rate by wolves on moose. Hares were abundant during 1990 and 1991, but crashed during winter (Krebs et al. 1995). We tested for effects of hare availability by comparing KGWD with $\log_{10}$ pack size, nested within the periods of presence and absence of snowshoe hares. Kill rate was not correlated with hare availability (nested ANOVA model, $F_{[1]} = 0.12$, $P = 0.91$).

Both DMK and $\log_{10}$ days/calf kill were not correlated with March snow depth (Table 2). Snow depth did not differ between years (ANOVA, $F_{[33]} = 0.66$, $P = 0.63$), ranging from 79 to 94 cm. The vulnerability of moose to predation by wolves increases when snow depths exceed 90 cm (Peter-

son 1977; Peterson et al. 1984). This snow depth was not exceeded in most winters.

We estimated consumption with an adjustment for raven scavenging (RA) and without (NRA). Based on the results of mock trials in our study area, Promberger (1992) estimated that ravens could remove 50% of ungulate biomass from a pair of wolves, 33% from a pack of 6 wolves, and 10% from a pack of 10 or more wolves. The NRA rate was 8.7 ± 0.9 (mean ± SE) kg/wolf each day, and was negatively correlated with $\log_{10}$ pack size ($r^2 = 0.40$, df = 44, $P < 0.0001$). Wolves in small packs apparently consumed 12.7 ± 1.5 kg/wolf each day, those in medium packs 7.6 ± 1 kg, and those in large packs 4.6 ± 0.3 kg.
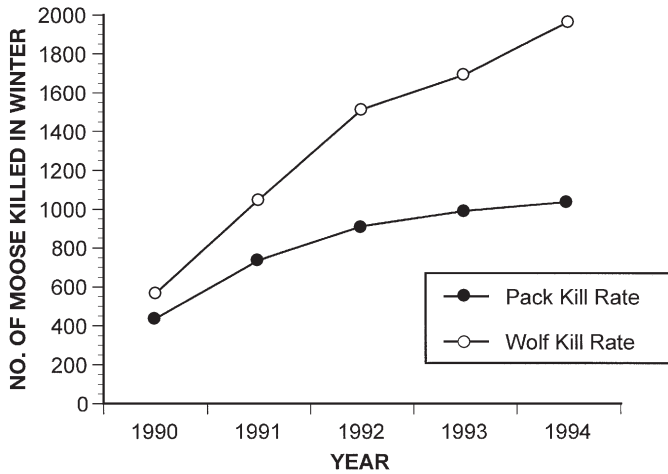
The RA rate remained correlated with $\log_{10}$ pack size, but pack-size differences were reduced ($r^2 = 0.13$, df = 44, $P = 0.014$). Raven scavenging reduced the available biomass to 6.4 ± 0.8 (mean ± SE) kg/wolf each day for small packs, 5.7 ± 0.9 kg for medium packs, and 4.1 ± 0.9 kg for large packs. The RA rate differed among the three pack-size classes (Kruskal–Wallis test, $\chi^2 = 6.1$, df = 2, $P = 0.04$).

Predation rate by wolves on moose

Small packs ($n = 17$ periods) killed 27 ± 2.4 (mean ± SE) moose each winter, medium packs ($n = 12$) 35 ± 3.8 moose, and large packs ($n = 14$) 46 ± 3.5 moose. We modeled winter predation on moose by applying these rates to packs with known composition each winter. As wolf packs in the area increased in number from 14 in 1990 to 24 in 1994 (see Table 2 in Hayes and Harestad 2000a), wolves increased their moose kills from 437 to 1037 (Table 3). For comparison, we modeled moose predation by applying the grand mean kill rate by wolves (0.045 moose/day for each wolf) and the number of wolves alive each winter (see Table 2 in Hayes and Harestad 2000a). The grand mean method yielded an estimated moose kill rate in 1994 that was nearly twice the pack kill rate (Fig. 5).

We estimated that wolves removed 10–15% of all moose and 7–16% of moose older than calves during winter (Table 3). We found a strong negative relation between annual wolf density (Table 2 in Hayes and Harestad 2000a) and the percentage of moose calves alive in March (Fig. 6; $r^2 = 0.86$, df = 4, $P = 0.02$). We found a similar relation for caribou calves (Fig. 6; $r^2 = 0.80$, df = 4, $P = 0.04$).

Fig. 5. Two models of wolf predation rates on moose, based on grand mean kill rates by wolves and pack-size kill rates during each year of the study.

Fig. 6. Relations between moose and caribou calf survival rates and wolf density in the FSA during each winter. The percentage of moose calves was estimated from March counts and the percentage of caribou calves from October counts (R. Farnell, unpublished data). The thick line shows the relation for caribou calves and the thin line shows the relation for moose calves.
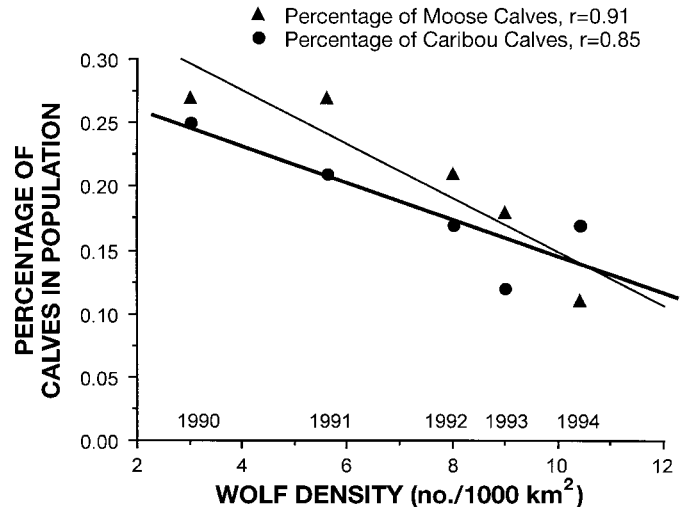

Discussion

Test of hypotheses

$H_0 1$: wolf predation represents additive mortality for prey populations. We found evidence to support our hypothesis that wolf predation represented additive mortality for both moose and caribou. Wolf predation is usually additive when prey are below the "nutrient-climate ceiling" (Theberge 1990; Gasaway et al. 1992). During our study, moose and caribou remained at low to moderate densities. Wolves in our study killed proportionally more calf, yearling, and old moose and fewer prime-age animals. This age pattern was similar to other Alaska and Yukon studies, where moose were also below the nutrient-climate ceiling (Fig. 7) (see Peterson et al. 1984; Ballard et al. 1987; Hayes et al. 1991; Gasaway et al. 1992).

Gasaway et al. (1992) estimated additive and compensatory mortality of moose on the basis of marrow-fat indices. Using his values, we found that 21 of 27 adults (77%) were in the largely additive mortality age-class (middle-aged). The remaining six were very old adults (>12 years of age) that we considered compensatory losses. Calves were also in the additive mortality class, but they showed lower marrow-fat indices than adults. These lower indices can be explained by the higher energetic requirements of calves for growth (Peterson et al. 1984). Both nutrition and age data are consistent with the hypothesis that wolf predation on moose was mainly additive. We had too few samples to estimate caribou condition.

$H_0 2$: the kill rate by wolves is dependent on prey density; $H_a 2$: the kill rate by wolves is independent of prey density and related to wolf-pack size. We found evidence for rejecting $H_0 2$ and accepting $H_a 2$. The kill rate by wolves was independent of moose density (Table 2) and pack size was the only variable of six tested that was related to kill rate. On average, large packs killed moose more often than did small packs, which is similar to the results of other studies (Ballard et al. 1987; Hayes et al. 1991; Thurber and Peterson 1993; Dale et al. 1994). Nevertheless, many of our small

Fig. 7. Ages of moose (excluding calves) killed by wolves during this study (FSA) and four other studies in Alaska and the Yukon. Other sources of data were as follows: Kenai Peninsula, Alaska, from Peterson et al. (1984); Nelchina, Alaska, from Ballard et al. (1987); Coast Mountains, Yukon, from Hayes et al. (1991); and Game Management Unit 20E, Alaska, from Gasaway et al. (1992).
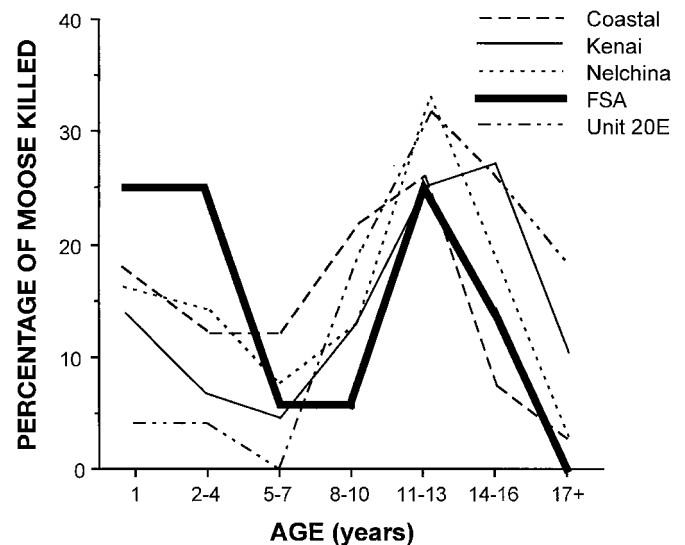
packs killed moose as often as larger packs did, which are similar to the findings of Hayes et al. (1991) and Thurber and Peterson (1993).

$H_0 3$: the kill rate by wolves on moose calves depends on the proportion of calves in winter populations. We obtained evidence for rejecting $H_0 3$. The kill rate on moose calves was not related to the number of calves available in winter, contrary to the findings of other studies (Peterson 1977;

Peterson et al. 1984). In most winters calves were abundant, but many vulnerable yearling moose were also available to wolves (Larsen and Ward 1995), apparently reducing calves' importance in wolves' diet.

$H_0 4$: the kill rate by wolves on moose is reduced when caribou availability exceeds that of moose. We had evidence for rejecting $H_0 4$. Wolves did not prey heavily on caribou that temporarily migrated into their pack territories, unlike wolves in Alaska (Dale et al. 1994, 1995). Wolves continued to kill mainly moose, even though caribou outnumbered moose and probably posed less of a risk to hunt (Haugen 1987). We believe that there was little benefit to preying on caribou because many calf and yearling moose were available in most winters and were also highly profitable and low-risk prey.

Snow depth, snowshoe hare availability, and search rate by wolves

Snow depth did not influence the rate at which wolves killed moose. Huggard (1993) and Mech et al. (1998) showed that snowfall can add substantial prey-density-independent variation to wolf predation rates. Low scavenging rates by wolves in all winters of our study indicated that snow depth probably did not reduce ungulate survival rates (Fuller 1991; Jędrzejewski et al. 1992; Huggard 1993). We conclude that winters were not severe enough to affect any measurable change in wolves' kill rates.

Snowshoe hare abundance had no detectable influence on the rate at which wolves killed moose. Snowshoe hares were abundant during 1990 and 1991, when moose and caribou were rapidly increasing, competition for ungulates was lowest, and many vulnerable, young moose and caribou were available. In this ecological context, we believe that there were few incentives for wolves to hunt snowshoe hares. Although wolves might survive on snowshoe hares during the peak of the cycle, they might not maintain the behavior necessary to enable them to defend large territories in winter.

Our data were consistent with those of Messier and Crête (1985) and Dale et al. (1995), who found that wolves' search rates were independent of prey density. Differences in prey density in our study might not have been sufficiently large to be detectable by the methods we used to measure search rates.

Consumption rate of wolves

Wolves' consumption rate was 8.7 kg/wolf/day, which is higher than rates estimated in previous studies (Thurber and Peterson 1993 and references therein). The apparent consumption rates for our study wolves were excessive. For example, wolves in small packs would have had to consume an average of 30% (12.7 kg) of their body mass each day of winter if they consumed all edible portions. Adjusting for biomass lost to ravens (RA) reduced our estimate of consumption to between 4.1 and 6.4 kg/wolf/day in packs of all sizes.

All packs handled moose carcasses in 2.6–3.3 days. Promberger (1992) found that large groups of ravens removed up to 37 kg of food/day from ungulate carcasses and he estimated that ravens removed proportionally more edible prey from small packs. Juvenile ravens form large cooperative flocks in winter (Heinrich 1991). These subadult flocks compete with small wolf packs because the small packs cannot handle kills as quickly as larger packs can. Other studies have shown that competition from scavengers can influence the kill rates of other carnivores (Harrison 1990; Cooper 1991). We believe that where ravens are common, they can have a significant impact on wolves' kill and consumption rates.

Optimal foraging-group size

The optimal foraging-group size was 2 wolves, which is similar to the findings of other wolf studies (Hayes et al. 1991; Thurber and Peterson 1993). Advantages for group-living carnivores include greater foraging efficiency (Bertram 1978; Nudds 1978), inclusive fitness (Bertram 1978; Rodman 1981), defense of young (Packer and Ruttan 1988), and protection of kills (Packer et al. 1990; Cooper 1991). Rodman (1981) argued that for larger wolf packs, the decline in foraging efficiency is offset by members improving their inclusive fitness through the addition of close relatives to the population (Rodman 1981). Schmidt and Mech (1997) argued that wolves live in packs primarily in order to share their kills with their young for kin-selection reasons, until younger wolves gain hunting and killing experience that improves their fitness after dispersal.

Predation rate by wolves on moose

We estimated that wolves killed 7% of moose older than calves in winter 1990 and 10–16% or more after 1991. These rates are higher than the annual adult mortality rates of 5–9% in stable or increasing moose populations in Alaska and the Yukon (Gasaway et al. 1983; Ballard et al. 1987; Larsen et al. 1989; Gasaway et al. 1992). In our study area, Larsen and Ward (1995) estimated a 5% mortality rate until the winter of 1992. Our predation-rate modeling predicted that wolves would reduce adult moose survival rates to levels that could not be sustained by recruitment.

Our results support the model of Walters et al. (1981), who found that the number of wolf packs was the best determinant of wolf predation rates. Higher kill rates by wolves in small packs enable them to remove a larger than expected proportion of moose from a population. The relatively high wolf predation rate in the early years of our study was related to the organization of wolves into many small packs whose kill rates were nearly equivalent to those of larger packs. Our results show that in order to model wolf predation rates, researchers need to know the number and sizes of wolf packs that are killing prey. Table 4 shows three hypothetical models of predation rates by 100 wolves on moose in winter, depending on different pack-size frequencies. Model 1 has the highest proportion in pairs (34%), and wolves removed 27% more moose than in model 3 which has 10% pairs, and 16% more than model 2, which has 20% pairs. In a stable wolf population, we could expect that pack density will not change but mean pack size will grow to about 10 wolves (Zimen 1976; Hayes and Harestad 2000*a*). Thus, using the same model parameters, 200 wolves organized into 20 packs in the same hypothetical area should kill about 920 moose during winter, only slightly more than in model 1 with half the number of wolves.

Although we found no other ecological determinants of kill rate beside wolf-pack size, kill rates could change if

Table 4. Three hypothetical models of predation rates by 100 wolves on moose in winter, depending on differences in pack-size frequency.

	Pack size	No. of wolves	No. of packs	Mean no. of moose killed in winter per pack	Total no. of moose killed in winter
Model 1	2	34	17	27	459
	6	36	6	35	210
	10	30	3	46	138
Total			26		807
Model 2	2	10	5	27	135
	6	30	5	35	175
	10	60	6	46	276
Total			16		586
Model 3	2	20	10	27	270
	6	30	5	35	175
	10	50	5	46	230
Total			20		675

some event (e.g., extremely deep or shallow snow) changes moose or caribou vulnerability to predation (Mech et al. 1998), or if the age or sex structure of a moose population changes with time, affecting fecundity or vulnerability to predation (Van Ballenberghe and Ballard 1997). A density-independent response can strongly influence prey selection and wolf functional responses (Huggard 1993; Mech et al. 1995), and other factors besides prey density should be measured when assessing wolf predation rates.

Data quality

Several factors could have confounded our estimates of kill rate. Caribou are available to more than half of the packs in summer and fall, but to fewer packs in late winter. By studying wolves in late winter we probably underestimated predation on caribou and overestimated predation on moose. We studied kill rates when moose were increasing from low to moderate densities ($0.26–0.44/km^2$). Kill rates cannot be expected to remain the same at lower moose densities (Messier 1994; Hayes and Harestad 2000b) in areas where relative densities of moose and caribou differ (Dale et al. 1995) or where other factors such as snow depth influence prey vulnerability (Mech et al. 1995). Our method of determining winter predation rates did not account for any spatial differences in moose in late winter, which we knew existed among wolf-pack territories (R. Florkiewicz, Yukon Fish and Wildlife Branch, Box 2703, Whitehorse, YT Y1A 2C6, Canada, unpublished data).

Acknowledgements

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Appendix

Table A1. Estimated moose density each winter in two regions in the Finlayson Study Area.

	North Canol area		Frances Lake area		
Winter	No. of moose/1000 km^2	Finite rate of change	No. of moose/1000 km^2	Finite rate of change	Mean moose density
1989–1990[a]	252	1.164	274	1.18	263
1990–1991[a]	293	1.164	323	1.18	308
1991–1992[b]	341	1.11	382	1.12	361
1992–1993[c]	379	1.10	427	1.10	403
1993–1994	417		470		443

[a]The finite rate of increase is interpolated from population estimates using stratified random block surveys in November 1987 (Jingfors 1988) and 1991 (Larsen and Ward 1995).
[b]The finite rate of increase is from Larsen and Ward (1995).
[c]The rate of increase is from Hatter and Bergerud (1991, see Methods), where R is 0.18 and M is the mean adult mortality rate (0.095; Larsen and Ward 1995).

Table A2. Composition of ungulate prey killed and kill rate by wolves in 21 packs monitored during late winter 1990 through 1994 in the Finlayson Study Area.

Year	Pack	No. of hours between locations	No. of wolves	No. of days studied	% of days observed	No. of moose killed	No. of caribou killed	Total mass of prey killed[a] (kg)	Mass of prey per wolf per day (kg)
1990	Frances L.	24	17	14	71	6	0	1 850	7.8
	Jackfish L.	24	2	31	84	6	0	1 125	18.1
	Ketza R.	48	2	31	65	3	0	700	11.3
	Lapie R.	48	5	30	53	5	0	1 676[b]	11.2
	Prevost R.	24	6	19	79	4	0	925	8.11
	Seven Wolf L.	24	2	38	89	2	1	452	6.0
	Tyers R.	48	2	20	60	2	0	800	20
	Tuchitua R.	24	11	36	75	5	0	1 725	4.4
	Weasel L.	24	6	16	81	5	0	1 513	15.8
	Woodside R.	24	4	39	77	7	0	2 063	13.2
	Yusezyu R.	24	2	30	87	6	0	1 163	19.4
	Upper Pelly R.	24	2	14	79	3	0	450	16.1
	Total		318			54	1	14 442	
1991	Finlayson L.	6	2	9	100	1	2	205	11.4
	Ketza R.	6	2	12	92	3	0	925	38.5
	Light Creek	48	2	6	67	1	0	150	12.5
	Mink Creek	6	4	11	100	1	3	869	19.8
	McEvoy L.	48	2	16	56	1	0	400	12.5
	Woodside R.	48	7	8	50	1	0	150	2.68
	Wolverine L.	24	2	9	78	2	0	813	45.2
	Seven Wolf L.	6	7	13	100	4	1	1 515	16.6
	Total		84			14	6	5 027	

Table A2 (*concluded*).

Year	Site								
1992	Campbell Creek	24	14	22	91	6	6	3 112	10.1
	Finlayson L.	24	2	28	57	5	0	1 450	25.9
	Fire Creek	48	3	24	50	3	0	800	11.1
	Frances L.	48	9	21	81	3	0	1 600	8.5
	Jackfish L.	48	11	23	48	6	0	2 150	8.5
	Ketza R.	48	2	19	63	3	0	1 200	31.6
	Light Creek	48	6	19	52	4	0	1 588	13.9
	Mink Creek	48	8	23	48	0	3	456	2.5
	Otter Creek	48	2	23	52	2	0	800	17.4
	Prevost R.	48	10	10	50	3	0	925	9.3
	Total			212		35	9	14 081	
1993	Seven Wolf L.	24	10	24	79	5	2	1 817	7.6
	Tuchitua R.	48	10	27	52	5	0	1 225	4.5
	Tyers R.	48	2	19	63	2	0	550	14.5
	Weasel L.	48	10	23	47	5	1	1 877	8.2
	Wolverine L.	48	2	21	52	3	0	950	22.6
	Woodside R.	48	11	24	58	4	0	1 350	5.1
	Yusezyu R.	48	11	33	48	7	0	1 788	4.9
	Total			171		31	3	9 537	
1994	Campbell Creek	24	20	27	96	11	2	3 442	6.4
	Mink Creek	24	11	26	92	4	1	1 752	6.1
	Light Creek	24	11	26	73	6	0	1 900	6.6
	Nipple Mt.	24	2	24	83	2	0	800	16.7
	Otter Creek	24	6	21	81	3	0	713	5.7
	Upper Pelly R.	24	5	21	81	3	0	1 200	11.4
	Wolverine L.	24	4	26	73	7	0	2 025	19.5
	Yusezyu R.	24	13	26	81	9	0	2 825	8.4
	Total			197		45	3	14 657	
	Grand total			982		179	25	57 764	

[a]Based on estimated masses (kg): cow moose 375, bull moose 413, unknown adult moose 400, yearling moose 250, calf moose 150, adult caribou 152, calf caribou 55, and mountain sheep 75. See methods for sources of live masses.
[b]Includes one mountain sheep.