

Wolf predation in a multiple-ungulate system in northern British Columbia

A.T. Bergerud and J.P. Elliott

Abstract: Caribou (*Rangifer tarandus*), elk (*Cervus canadensis*), moose (*Alces alces*), and Stone's sheep (*Ovis dalli stonei*) were either decreasing or stable in numbers in two areas in northeastern British Columbia in 1981–1982, prior to reductions in wolf (*Canis lupus*) numbers. Following the reduction of wolf numbers, recruitment improved 2–5 times for all four species, and all populations increased, based on either hunting statistics, census results, and (or) recruitments greater than 24 offspring at 9 months of age per 100 females. Recruitment of offspring at 9 months of age, when regressed against wolf numbers, declined with decelerating slopes for all four species. This inverse functional response is hypothesized to result from the preparturient spacing of females to reduce predation risk, and in this regard moose seem the least secure and sheep the most effectively spaced. For the four species, mean recruitment at 9 months of age that balanced adult mortality and provided a finite rate of increase of 1.00 was 24.16 ± 0.91 offspring/100 females ($n = 11$, coefficient of variation = 12.5%). The predicted recruitment rate for all four species in the absence of wolves was 53–57 offspring/100 females. But the birth rate of moose was much higher than those of the other species, indicating greater loss to other factors of which bear predation may be the greatest. Following wolf reductions of 60–86% of entire travelling packs, the wolves quickly recolonized the removal zones, with rates of increase ranging from 1.5 to 5.6.

Résumé : En 1981–1982, avant la diminution du nombre de Loups gris (*Canis lupus*), les populations du Caribou (*Rangifer tarandus*), du Wapiti (*Cervus canadensis*), de l'Orignal (*Alces alces*) et du Mouflon de Stone (*Ovis dalli stonei*) étaient en déclin ou étaient stables en deux régions du nord-est de la Colombie-Britannique. À la suite de la réduction du nombre de loups, le recrutement a augmenté par un facteur de 2 à 5 chez les quatre espèces et toutes les populations ont connu un essor d'après les statistiques de chasse et les inventaires ou lorsque le recrutement de jeunes à l'âge de 9 mois/100 femelles dépassait 24. Le recrutement de jeunes de 9 mois diminuait chez les quatre espèces en fonction du nombre de loups selon une pente de moins en moins accentuée. Il se peut que cette réaction fonctionnelle renversée soit le résultat de l'espacement des femelles avant la parturition pour réduire les risques de prédation et, sous cet aspect, les orignaux semblent les animaux les moins protégés et les mouflons, les animaux à l'espacement le plus efficace. Chez les quatre espèces, le recrutement moyen à 9 mois, qui peut contrebalancer la mortalité des adultes et donner lieu à un taux fini d'augmentation de 1,0, a été évalué à $24,6 \pm 0,91$ jeunes/100 femelles ($n = 11$, CV = 12,5%). Le taux théorique de recrutement pour les quatre espèces en l'absence des loups a été évalué à 53–57 jeunes/100 femelles. Mais le taux de natalité s'est avéré beaucoup plus élevé chez les orignaux que chez les autres espèces, ce qui indique qu'il existe d'autres facteurs de perte, dont la prédation par les ours est sans doute le plus important. Après réduction de 60–86% de leur nombre dans les meutes entières en déplacement, les loups ont vite fait de recoloniser les zones évacuées à raison de 1,5 à 5,6.

[Traduit par la Rédaction]

Introduction

Predation by wolves (*Canis lupus*) and bears (*Ursus arctos*, *Ursus americana*) is now recognized as a major limiting factor in the growth of moose (*Alces alces*) and caribou (*Rangifer tarandus*) populations in northern ecosystems in North America (Pimlott 1967; Bergerud 1974; Keith 1974, 1983; Gasaway et al. 1983, 1992; Bergerud et al. 1984; Messier and Crete 1985; Bergerud and Elliott 1986; Ballard and Larsen 1987; Van Ballenberghe 1987; Adams et al.

1995a, 1995b; Page 1988; Bergerud 1988, 1992, 1996; Larsen et al. 1989a, 1989b; Ballard et al. 1991; Messier 1991, 1994; Van Ballenberghe and Ballard 1994; Boertje et al. 1996). The densities of both moose and caribou in noninsular situations are generally less than $0.4/\text{km}^2$ when they share the range with only lightly exploited bear and wolf populations (Bergerud 1980; Crête 1987; Bergerud and Snider 1988; and Gasaway et al. 1992) (an exception is insular Isle Royale, Michigan; Peterson 1977). In the absence of wolves, caribou numbers, when prorated to the entire annual range, frequently exceed $1/\text{km}^2$ (Bergerud 1980, 1992; Skogland 1985) and moose densities commonly exceed $1.5/\text{km}^2$ (Bergerud and Manuel 1969; Blood 1974; Bailey 1978; Albright and Keith 1987; Gasaway et al. 1992). Crête (1989) has estimated the intrinsic K (food limitation) for moose in eastern North America at $>2.0/\text{km}^2$ and Messier (1994) has calculated an equilibrium density of $2/\text{km}^2$ in systems in North America without predators.

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The answer to the question of whether the predation deaths of young ungulates 0–12 months of age is density-dependent or density-independent is not as clear as the answer to whether predation is a limiting factor. Three studies of bear predation of moose calves have indicated that bear predation is density-independent (Boertje et al. 1988; Larsen et al. 1989a; Ballard et al. 1991). Conversely, in one study, predation by wolves on moose calves and adults in three areas showed an increase in mortality rates between low and high moose densities (Messier and Crête 1985). If young ungulates are dispersed and sedentary in the spring and summer, one might expect that as predation proceeded and was sufficient that prey numbers declined, the remaining animals would be more widely spaced, which would reduce encounter rates with searching predators (Taylor 1976) and decrease mortality rates (Bergerud and Page 1987).

In this study we tested the limiting effect and density dependence of wolf predation in the survival of young animals, not only for the two most widely investigated species, moose and caribou, but also in a multiple-ungulate system in British Columbia that included Stone's sheep (*Ovis dalli stonei*) and elk (*Cervus canadensis*). All four species were lightly hunted, <3% per year (British Columbia harvest statistics). We tested for limiting effects and density dependence of wolf predation for all four species by regressing recruitment (number of offspring per 100 females) at 5–9 months of age against a range of wolf densities that we modified by wolf-removal experiments. If the regressions were curvilinear, with survival decreasing at a decreasing rate (concave curves) as the number of recruits was reduced, this would support the conclusion of a density-dependent response.

Further, we evaluated four hypotheses as to the role of snow cover on offspring survival, using multiple regressions with snow statistics and wolf numbers. These hypotheses were as follows: (1) that excessive winter snow resulted in starvation (not tested for caribou), (2) that offspring mortality increased in years with more snow in the spring because the dispersal of preparturient females to reduce encounters with predators was restricted (Bergerud and Page 1987), (3) that excessive winter and spring snow cover infringed on the nutritional status of females, affecting neonate viability and vulnerability to predation (Adams et al. 1995a), and (4) that excessive winter snow depths resulted in surplus killing by wolves (Eide and Ballard 1982; Dale et al. 1995; Mech et al. 1995).

We tested the hypothesis that the prey biomass determined the abundance of wolves (Van Ballenberghe et al. 1975; Fuller 1989; Messier 1994). By quantifying both wolf and prey abundance we could check if they were positively correlated and in agreement with predictions from Fuller's (1989) equation of the number of wolves per 1000 km² regressed on a ungulate biomass index that he constructed on the basis of data from 25 North American studies.

Study areas

Two major study areas in northeastern British Columbia were the Kechika (18 400 km²), 58°45'N, 128°W, and the Muskwa (19 000 km²), 58°N, 124°W (Fig. 1). Two control areas for the Kechika were Blue Jennings (6500 km²), 130°30'N, 59°30'W, and

Deer Trout (3046 km²), 59°N, 126°W. Wolves and bears were common in all these areas.

In the Kechika our concern was the role of wolf predation on the dynamics of sheep and moose and a small herd of caribou in the Horseranch Mountains (Bergerud and Elliott 1986). Also a small herd of introduced elk (<200) was present. The Kechika is bisected by the Rocky Mountain trench, with elevations of 600–900 m. Maximum elevations reach 2300 m. Sheep were found primarily on the west side of the valley and occupied 5000 km² in midwinter, when we counted animals. Moose occupied the entire area, except that during the winter they were generally below treeline (~1300 m), in an area of about 9000 km².

The Muskwa had a greater diversity of ungulates than the Kechika, with elk, moose, caribou, Stone's sheep, mountain goats (*Oreamnis americanus*), mule deer (*Odocoileus hemionus*), and buffalo (*Bison bison*) (in the southern portion) all present. Our major concern was the dynamics of moose, sheep, and elk, but we also measured the recruitment of some cohorts of caribou. The elk occupied an area of ~3000 km² and sheep ranged over 10 000 km². The continental divide formed part of the western boundary, with elevations reaching 2900 m. These high peaks resulted in a snow shadow for the Muskwa foothills to the east that resulted in a mean depth of snow on March 1 from 1977–1978 to 1985–1986 of only 26.7 cm (extremes 15–50 cm) (Peck 1988). It was this low snow cover that permitted the presence of elk and deer at these northern latitudes.

A minor study area used to check the density of wolves with a depauperate prey base was Nelson (21 177 km², 59°N, 123°W), where we censused moose and wolves only in 1988. Nelson is a lowland muskeg habitat stretching from the foothills east to Alberta (Fig. 1). Moose are at low densities and possibly 200 caribou (0.01/km²) are widely scattered. Bears are also rare. The region is crisscrossed by seismic lines through the rather open boreal coniferous forest.

Methods

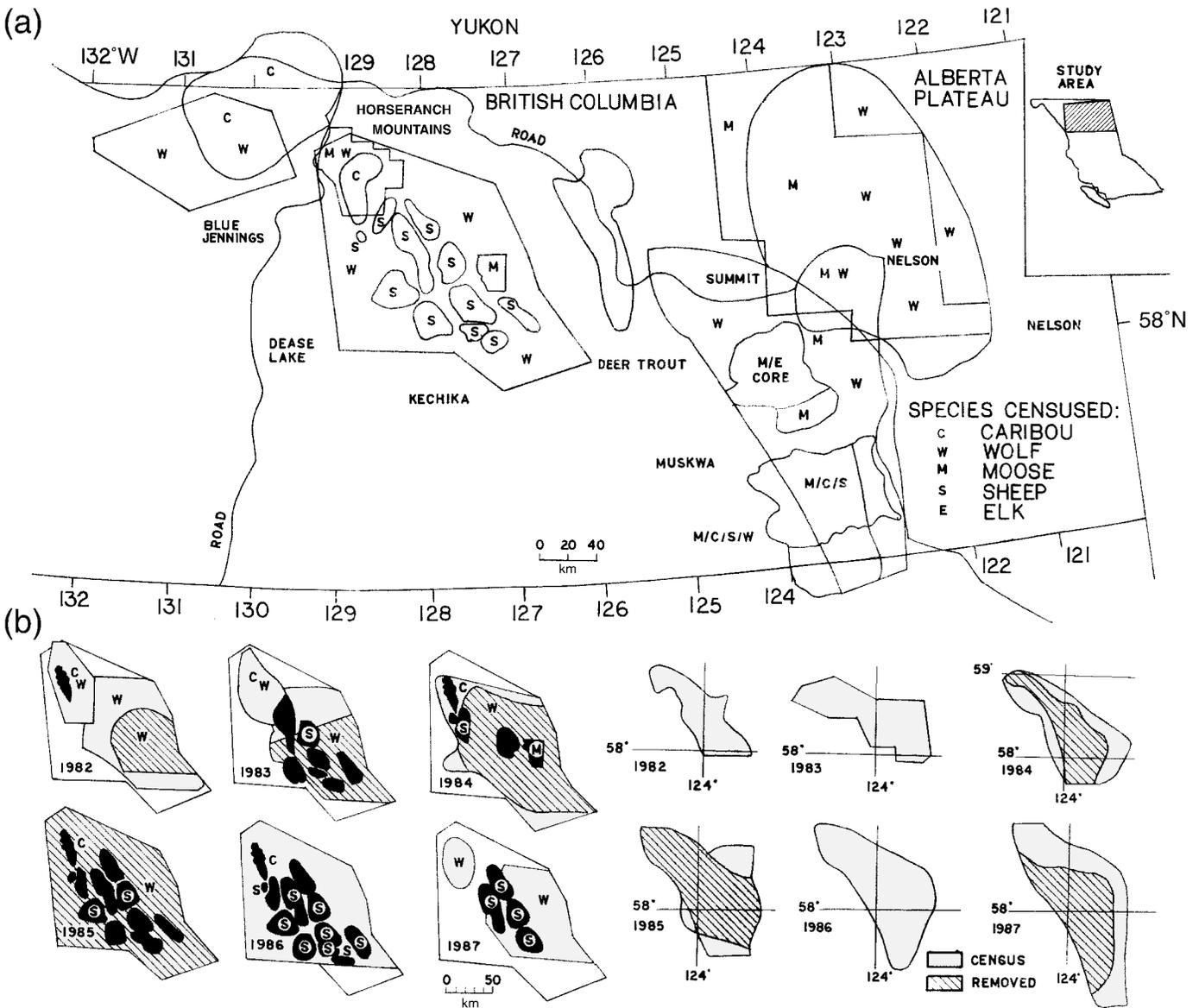
Census of wolves

Wolves were censused in late winter in all the areas by helicopter surveys. The areas censused varied in size between years and sizes are shown in Fig. 1. These inventory procedures followed the aerial census methods developed by Stephenson (1978) in Alaska and refined by Hayes et al. (1989) in the Yukon. But we applied no correction factor for single wolves that were overlooked. These investigators worked in habitats with similar topography and forest cover to northern British Columbia and verified their counts in some cases with radiotelemetry studies.

The aerial search patterns involved flying along likely wolf travel routes (ridges, lakes, and streams and areas of low snow cover). The flights were made with two observers 24–48 h after a fresh snowfall. When fresh sign was encountered the tracks were followed until the wolves were located or their tracks separated sufficiently to enable complete counts.

Following the censuses, wolves were removed in March–April by shooting in some years as follows: the northern Kechika (Horseranch Mountains): 23 of 36 (61%) from 3600 km² in 1978, 25 of 29 (86%) from 3600 km² in 1979, and 23 of 27 (85%) from 5200 km² in 1980 (Bergerud and Elliott 1986) (an additional 70+ wolves were removed from an area of unknown size in 1987 by hunting guides); the Kechika: 70 of 88 (85%) from 3833 km² in 1982, 89 of 107 (83%) from 7123 km² in 1983, 105 of 138 (76%) from 9961 km² in 1984, and 157 of 242 (65%) from 18 400 km², including the Horseranch Mountains, in 1985; the Muskwa: 182 of 303 (60%) from 6775 km² in 1984, 198 of 256 (77%) from 13 570 km² in 1985, and 125 of 210 (62%) from 10 000 km² in

Fig. 1. (a) The overall study areas. (b) Areas where wolves were removed in the Kechika (left) and the Muskwa (right).



1987. Also, the wolf population in the Muskwa had been reduced as late as 1979–1980 by local outfitters and guides.

Recruitment of ungulates

Ungulates were classified as to sex and age by helicopter surveys in either the fall (young, ~5 months of age) or in March, when the new generation was ~9 months old. The sex and age classes recognized are shown in Table 1. Recruitment was expressed as the number of calves 5–9 months of age per 100 females (females ≥17 months of age) or yearlings 17–21 months of age per 100 females (females ≥29 months of age). The ratio of lambs was calculated per 100 ewes + male yearlings; the number of male yearlings was assumed to equal that of female yearlings. For moose and elk yearlings (17- to 21-month indices), we doubled the male yearlings counted and corrected the total of adult females by subtracting the actual number of male yearlings counted. For sheep we had to double the totals of female yearlings to account for male yearlings that were confounded with adult females and correct the totals of females by subtracting the actual number of fe-

Table 1. Sex and age composition of ungulates classified.

	November 1	March 1
Moose	M ^{≥29} , F ^{≥17} , C ⁵ , MYr ¹⁷	M ^{≥21} , F ^{≥21} , C ⁹
Elk	M ^{≥29} , F ^{≥17} , C ⁵ , MYr ¹⁷	M ^{≥33} , F ^{≥21} , C ⁹ , MYr ²¹
Sheep	Not determined	M ^{≥33} (F ^{≥33} + MYr ²¹), L ⁹ , FYr ²¹
Caribou	M ^{≥17} , F ^{≥17} , C ⁵	M ^{≥21} , F ^{≥21} , C ⁹

Note: M, male; F, female; C, calf; Yr, yearling; L, lamb. Superscripts indicate the approximate age in months.

male yearlings counted. In classifications in which animals of only one sex (17 or 21 months of age) were recognized (female yearling ewes and male yearling moose and elk), the assumption was that the numbers of males and females still alive in the new cohort were equal. This assumption is not valid for caribou in northern British Columbia (Bergerud and Elliott 1986), and our basic measure of recruitment, *R*, was the number of calves 5 or 9 months of

age. A problem with the use of calves instead of yearlings is that for sheep and elk, the calves are still more vulnerable to predation than adults and thus the R value at 9 months of age could underestimate the final recruitment, which should be measured when the mortality rate of the new generation equals that of adults (Hickey 1955).

The total numbers of moose and elk classified generally included at least 200 females. Many of the classifications of sheep and caribou involved nearly all the population concentrated on fall rutting or winter ranges. The classifications of moose and elk were based on systematic flight lines across a large proportion of the Kechika and Muskwa. In the Muskwa, flight lines were 2–5 km apart for moose and 2.5–5 km apart for elk. In the Kechika the lines for moose were at 3-km intervals. The same flight patterns were followed each year.

Census of ungulates

Moose and elk populations that were censused were tallied using the stratified random block technique (Gasaway et al. 1986). Surveys included the enumeration of elk and moose in naturally bounded habitat blocks varying in size from 1 to 33 km²; the same blocks were used in repeat counts of moose in Middle Creek, Kechika, in 1984 and 1988 (28% of the census area) and for moose and elk in the Muskwa in 1982, 1985, and 1989 (13.5% of the census area) and Nelson (10.2%) in 1988.

Surveys were conducted in late winter (February and March), in good snow and light conditions, using a Bell 206 helicopter with two observers. The census blocks were usually searched by flying the boundaries of the block and spiralling inward.

In the winter, moose have a tendency to concentrate on lowland ranges with reduced snow depths. The representation of the selected late-winter census areas was evaluated by comparing the distribution of moose aggregations in November (from the transects to determine recruitment) with similar transects flown in March. The area censused for elk included nearly all the area where elk wintered in the Muskwa.

Complete counts of subpopulations for 10 subsections of the Kechika sheep population were made in 8 years; in some years only 3 subsections were counted, in other years all 10 were evaluated. Each section was an isolated mountain range separated from other units by intervening river valleys. The sheep were inventoried from a helicopter on clear, calm days when the temperature was commonly -20° . Complete units were searched through all habitat types and elevations by contour flying. If fresh sign was found, the search was continued until the animals were located. One subpopulation was censused on 5 different days within a week to evaluate the precision of the counts.

The caribou in the north Kechika (Horseranch Mountains) were censused by helicopter using complete counting methods each October during the rutting season (Bergerud and Elliott 1986). Searches were made using contour flying in which all the range above treeline was viewed. It was generally possible to see animals on the previous flight line when the adjacent flight line came abreast of these concentrations.

To determine if moose and elk populations had changed in size between censuses we compared the total numbers of animals seen in the same blocks between surveys. A t test of difference was used to test significance. This technique involves fewer assumptions than stratifying the results and calculating confidence limits. In these surveys there was no correction factor for animals missed, hence the mean was not an unbiased estimator of the true population, μ (Gasaway and DuBois 1987; Bergerud and Snider 1988).

Indices of population change

Indices of change (finite rate of change, λ) were based on (i) the census data, (ii) a comparison between years of the hunting success

of hunters securing an animal and the total number of days required to harvest an animal, and (iii) calculation of a statistic we call stabilizing recruitment (R_s) and comparison of R_s with the observed R value for that cohort. R_s is defined as the number of offspring 5 or 9 months of age per 100 females that balanced the total mortality of adults in lightly hunted populations (<5% annual harvest) (Bergerud 1992). R_s was estimated by regressing λ values from the census data on the observed R values that contributed to the population change between the counts and then calculating from the linear regression equation the number of calves per 100 females that gave $\lambda = 1.00$.

The λ values based on census results of the R_s analysis were 2 for elk in the Muskwa, 3 for moose in the Kechika and Muskwa, 8 for caribou in the Kechika, and 14 for the sheep subpopulations in the Kechika. Because of the limited census results we searched the literature for other studies in North America where wolves were present, both λ and R had been measured, and mortality from hunting was <5%. We found four such studies of moose (49 data points), one study of caribou (15 points), one of elk (5 points), and one of sheep (12 points). We compared the slope of these regressions from outside British Columbia (λ on R) with the data from northern British Columbia to determine if differences existed or if, in fact, widespread populations in Canada and Alaska might have R_s values similar to those in British Columbia, in which case we could place more confidence in our restricted samples.

Snow statistics

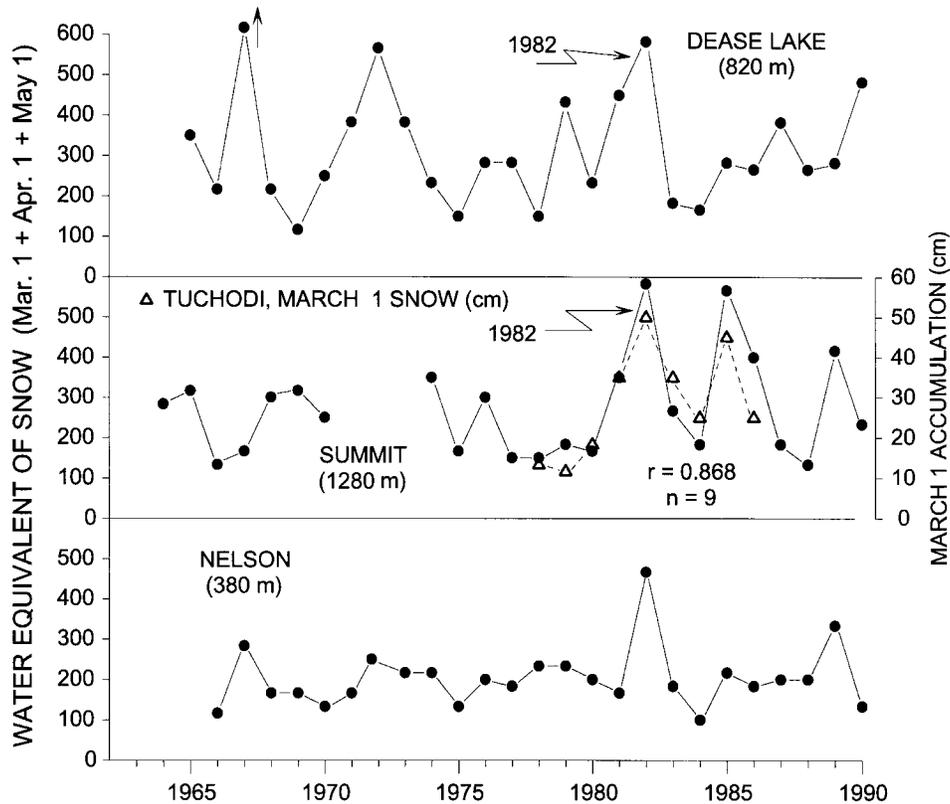
Snow statistics used in multiple regressions for the recruitment analysis for the Kechika were secured from the Dease Lake weather station (820 m elevation), 70 km from the Kechika. For the Muskwa, snow statistics were from the Summit station located within the Muskwa at 1280 m elevation. Further, Peck (1988) recorded snow depths in the Tuchodi River valley in the Muskwa (an area where the elk were concentrated in the winter) for the years 1978–1986. The index from the weather stations that we used was the water equivalent of the snowpack recorded at the beginning of March, April, and May (Fig. 2). The water-equivalent index should reflect energy expenditures of ungulates more closely than snow depth, since it incorporates both depth and density, which influence sinking depth (see Parker et al. 1984; Antifeau 1987). The water-equivalent index also reflects spring melting rates better than snow depth because it includes density, and we were interested in the percentage of the ground that was free of snow at parturition to allow dispersal of females. Snow depth and the water-equivalent index are highly correlated (see Fig. 2).

Findings

Wolf numbers and pack size

The densities of wolves prior to reductions were 10/1000 km² for the northern Kechika (Horseranch Mountains) in 1978 (Bergerud and Elliott 1986), approximately 15.5/1000 km² for the middle and southern Kechika in 1982, and 15.5/1000 km² for the control population at Blue Jennings in both 1985 and 1986 (Fig. 3). The densities were lower for the Muskwa, <10 wolves/1000 km² in 1978–1980, and there were only 4.1/1000 km² at Nelson in 1988. The low density in Muskwa from 1978 to 1980 resulted from wolf reductions by local outfitters. These reductions ceased after 1980 and the population increased at a finite rate of increase of 1.47, reaching 39 wolves/1000 km² in 1984, prior to our first reduction. At the end of the study, the overall density for the Kechika was 17.5/1000 km² in 1987 and 22/1000 km² in the Muskwa in 1990 (Fig. 3).

Fig. 2. Snow statistics used in this study.



One problem with the wolf census results is that densities generally decreased as the size of the census area increased, especially in the Kechika (Fig. 3). The central area in the Kechika (3833 km²) always had more wolves than adjacent areas. Presumably there was a bias towards selecting census and removal areas that had high numbers of wolves. A bias could also have resulted if the study areas were selected because of the abundance of ungulates; such habitats would have a concentration of wolves. As a census area was increased it would naturally include an increasing proportion of elevated terrain, which would lower the results because of the concentration of wolves at low elevations along river valleys.

The census results appear to be reasonably accurate. The counts in the Kechika and Muskwa were partly verified from the number of wolves removed. Obviously there had to be at least that many wolves. In 2 of the 3 years (1982–1984) in which repeat counts were made after removal, the counts agreed with the preremoval total minus the number removed. In the third year there were supposed to be 33 wolves left after removal but the repeat census failed to locate any (originally 138, 105 removed, leaving 33). Thus, there is a possibility of overcounting when this method is used, as well as the obvious possibility of missing animals, especially singletons. This technique is the standard method used in Alaska and the Yukon, but those researchers use fixed-wing aircraft. In British Columbia only helicopters were used and results should be more accurate.

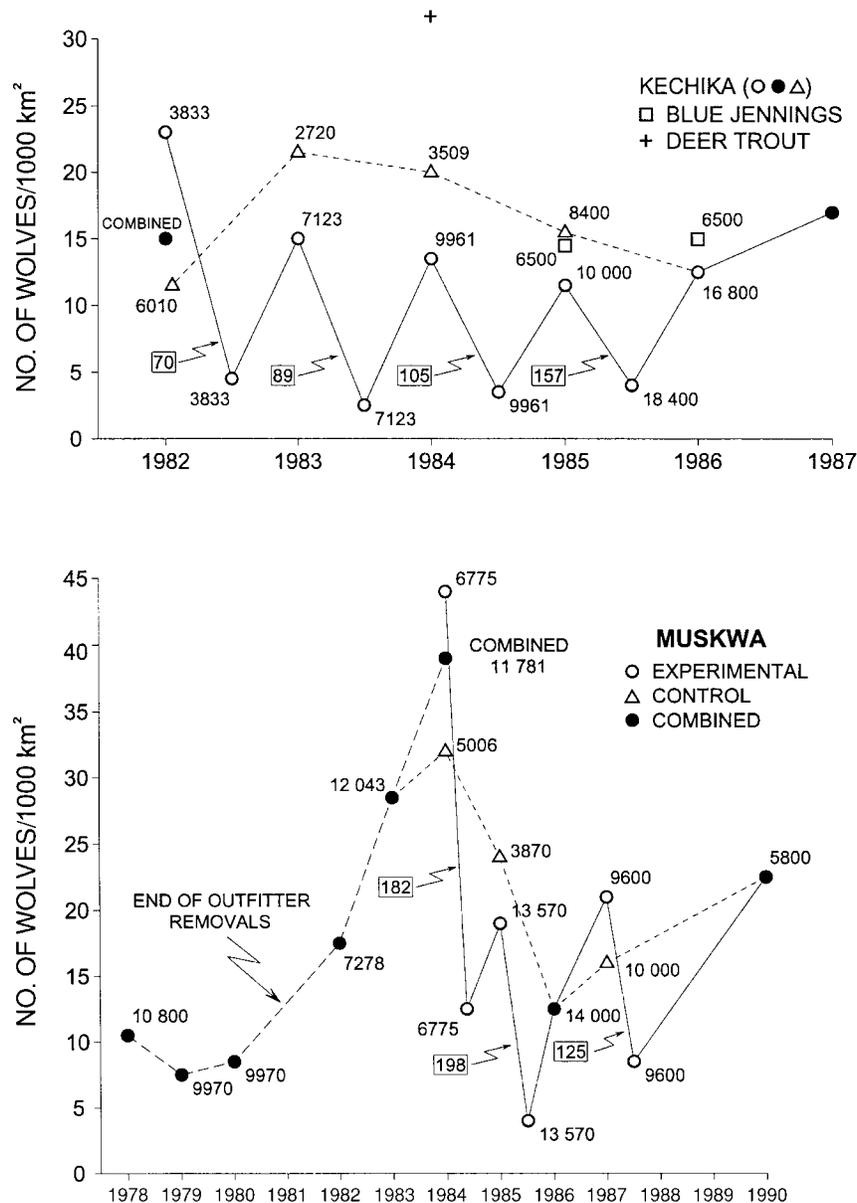
The percentages of the wolves removed from the experimental areas were $77 \pm 4.4\%$ (SE) from the Kechika in

1982–1985 ($n = 4$) (421 wolves) and $66 \pm 5.7\%$ from the Muskwa in 1984–1985 and 1987 ($n = 3$) (505 wolves) (we reported previously the removal from the Horseranch Mountains; Bergerud and Elliott 1986). The lowest removal rates were 60 and 62% in the Muskwa in 1984 and 1987 (Fig. 3).

Each year following the reductions, the wolf populations had made a considerable recovery by the time that they were recensused in the following February–March (Fig. 3); this recovery sequence has also been documented in Alaska (Ballard et al. 1987) and the Yukon (Hayes et al. 1989; Larsen et al. 1989a). Recovery figures are not precise, since the censused areas and removal areas changed in size between years. If we consider that the Kechika had 15.5 wolves/1000 km² in 1982, then the recovery rates by the next winter were 97% in 1983, 90% in 1984, 72% in 1985, and 81% by 1986. For the Muskwa, using the density in 1983, which was 28.7/1000 km², rather than that in 1984 (the latter seems excessive, based on prey biomass; Fuller 1989), the recovery rate was 66% after the 1984 removal, 45% after the 1985 reduction, and 73% after 1987; the density in 1990 was 77% of that in 1983 (Fig. 2). The recovery rate was lower in the original core removal areas, where reductions occurred during all seven removal programs (Table 2).

The rationale for increasing the size of the removal areas in the Kechika in subsequent years, 1982–1985, was to reduce the ingress of wolves in the year following removal. But the sizes of the removal areas in the Kechika and Muskwa were not clearly correlated with the rate of increase the following year ($Y = 4.409 - 0.0001X$, where Y is the rate

Fig. 3. Census estimates for wolves during the winter season in the Kechika, Blue Jennings, Deer Trout, and the Muskwa. Numbers adjacent to the data points show the size of the census area (km²); numbers in boxes show the number of wolves removed.



of increase and X is the size of the area; $r = -0.374$, $n = 6$). More important for recovery was the percentage of wolves removed; the more that were taken, the more moved into the vacant area ($Y = -5.572 + 0.120X$, where X is the percentage removed; $r = 0.825$, $P < 0.05$, $n = 6$). This sequence also occurred when wolves were removed from the Finlayson caribou herd in the Yukon (Farnell and McDonald 1988; Hayes et al. 1989).

The percentage of single and duo wolf aggregations of the total aggregations in undisturbed areas was $\leq 30\%$ (Fig. 4). For populations disturbed by removals, the percentage of singletons and duos in the following year usually exceeded 30% (Fig. 4), whereas for populations adjacent to removal areas (controls), the percentages of singletons and duos ranged from 20 to 35%, with one exception (Fig. 4). The

rate of increase from years Y_1 to Y_2 was correlated with the percentage of singletons and duos the following year (Y_2) (Fig. 4), which indicates that the small aggregations were not resident wolf packs that had fragmented during removals, but mostly colonizing wolves.

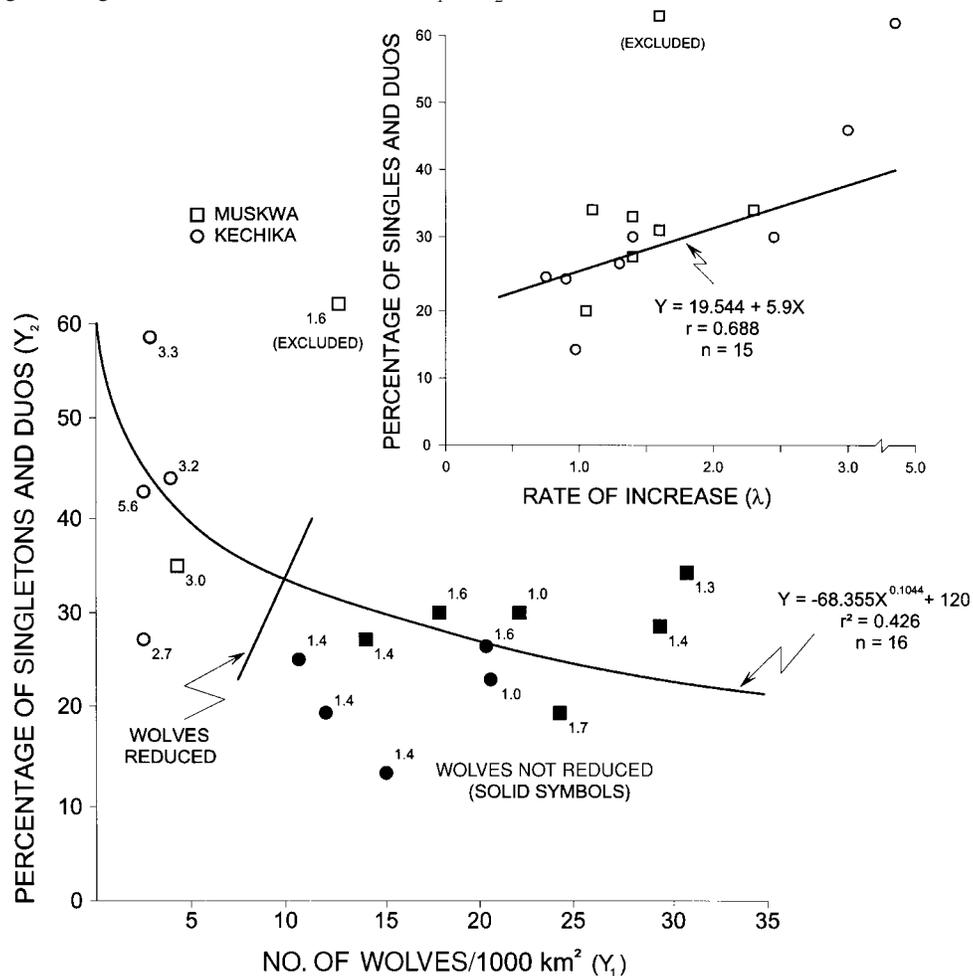
The mean group size (>1 wolf) was reduced by 2 wolves prior to removal when the undisturbed size is compared with pack size after removal in the Kechika and Muskwa (6.4 ± 0.29 ($n = 8$) vs. 4.4 ± 0.20 ($n = 13$)). Presumably, the colonizing wolves were mostly young animals that were not accompanied by progeny. In both the Kechika and the Muskwa, wolf aggregations remained small 2 years after removal. In the Muskwa, packs were still small in 1990, 3 years after the last reduction in 1987, and the density of 22/1000 km² was less than during the peak in 1984

Table 2. Wolf aggregations observed in winter before removal in the core areas.

Observed group size	Percentage of packs observed									
	Kechika (3833 km ²)						Muskwa (6775 km ²)			
	1982	1983	1984	1985	1986	1987	1984	1985	1986	1987
1	—	25	31	26	5	—	19	28	18	11
2	8	19	23	42	21	21	12	35	21	20
3	15	13	15	5	21	14	14	15	14	17
4	—	6	15	—	21	7	15	9	18	20
5	8	19	—	11	11	14	12	11	11	14
6	8	—	8	11	5	21	7	2	14	14
7	23	6	—	5	—	—	7	—	—	—
8	23	—	8	—	11	—	7	—	4	3
9	—	6	—	—	—	14	2	—	—	—
10	8	—	—	—	—	—	2	—	—	—
>10	8	6	—	—	5	7	5	2	—	—
Total no. of groups	13	16	13	19	19	14	59	46	28	35
Total no. of wolves	88	63	38	53	81	80	302	125	96	127
No. of wolves/1000 km ²	22.9	16.4	9.9	13.8	21.1	20.9	44.6	18.5	14.2	18.7

Note: Wolves were removed in Kechika in 1982, 1983, 1984, and 1985 and in Muskwa in 1984, 1985, and 1987.

Fig. 4. Percentages of single and duo wolf aggregations (Y_1) regressed against wolf densities (Y_1) and percentages of single and duo aggregations (Y_2) regressed against the rate of increase from Y_1 to Y_2 .



(39/1000 km²) prior to removal. However, wolf densities in the Kechika in 1987 had increased beyond the preremoval level of 15–18/1000 km².

Wolves were removed from the central area in the Kechika (3833 km²) in 4 consecutive years. The number of groups per 1000 km² showed no consistent downward pat-

Table 3. Recruitment (number of offspring per 100 females) of moose and sheep in the Kechika and Muskwa between cohorts when wolves were reduced and not reduced prior to birth.

	5 months of age		9 months of age		17 or 21 months of age ^a	
	Wolves not reduced	Wolves reduced	Wolves not reduced	Wolves reduced	Wolves not reduced	Wolves reduced
Moose						
Kechika						
1981	—	—	14.1 (543)	—	21.5 (78)	—
1982	14.0 (86) ^b	33.3 (147)	10.8 (83)	31.1 (135)	15.9 (63)	38.2 (246)
1983	5.9 (68)	48.8 (293)	7.1 (71)	43.8 (121)	10.8 (74)	33.1 (151)
1983	—	—	8.8 (68) ^c	—	—	—
1984	7.7 (74) ^c	43.2 (176)	5.1 (78) ^c	49.4 (164)	0.0 (74) ^c	46.2 (134)
1985	12.2 (74) ^c	46.7 (165)	4.4 (68) ^c	33.7 (156)	0.0 (79)	42.4 (99)
1986	20.1 (120)	—	—	—	—	—
1987	—	—	31.1 (61)	—	—	—
1988	—	—	27.5 (120)	—	—	—
Mean	12.0±2.11	43.0±3.29	14.4±3.29	39.5±4.29	8.2±3.48	40.0±2.81
Muskwa						
1982	—	—	12.6 (282)	—	—	—
1983	—	—	9.0 (211)	—	10.9 (440)	—
1984	—	28.7 (464)	—	33.3 (196)	—	25.1 (549)
1985	—	40.6 (618)	—	30.4 (138)	—	20.1 (497)
1986	26.0 (547)	—	23.3 (150)	—	25.0 (376)	—
1987	—	20.3 (423)	—	31.4 (216)	—	—
1988	—	—	30.4 (1232)	—	—	—
1989	—	—	27.3 (476)	—	—	—
Mean	26.0	29.9±5.89	20.5±4.16	31.7±0.85	18.0±7.05	22.6±2.50
Sheep						
Kechika						
1981	—	—	—	—	17.9 (691)	—
1982	—	—	19.2 (334)	41.1 (419)	20.4 (49) ^c	32.0 (300)
1983	—	—	18.2 (308)	49.1 (318)	16.1 (285)	45.3 (578)
1983	—	—	—	—	8.3 (144) ^c	—
1984	—	—	18.4 (54) ^c	—	18.6 (65)	—
1984	—	—	20.7 (150)	—	—	—
1984	—	—	21.1 (71)	44.6 (709)	15.4 (91)	48.0 (754)
1985	—	—	23.5 (91)	43.3 (941)	—	21.1 (627)
1986	—	—	23.4 (693)	—	11.1 (108)	—
1987	—	—	14.0 (144)	—	24.4 (237)	—
1988	—	—	25.2 (266)	—	—	—
Mean	—	—	20.4±1.14	44.5±1.69	16.5±1.80	36.6±6.23
Muskwa						
1981	—	—	36.5 (123)	—	15.1 (292)	—
1982	—	—	30.3 (314)	—	7.2 (333)	—
1983	—	—	21.1 (345)	—	17.5 (571)	—
1984	—	—	—	35.7 (222)	—	41.0 (200)
1985	—	—	—	30.7 (241)	—	12.3 (162)
1986	—	—	14.5 (172)	—	27.0 (259)	—
1987	—	—	—	49.3 (294)	—	—
1988	—	—	—	—	—	—
1989	—	—	13.1 (844)	—	—	—
Mean	—	—	23.1±4.50	38.6±5.56	16.7±4.08	26.7±14.35

Note: GLM test: moose age, $F = 0.78$, $P = 0.381$; area, $F = 0.16$, $P = 0.691$; wolves reduced/not reduced, $F = 63.05$, $P = 0.0001$; sheep age, $F = 5.85$, $P = 0.021$; area, $F = 0.33$, $P = 0.571$; wolves, $F = 48.75$, $P = 0.0001$. Numbers in parentheses show the number of cows or ewes.

^aSeventeen months for moose, 21 months for sheep.

^bEighty-six females in the sample.

^cBlue Jennings and (or) Deer Trout.

Table 4. Recruitment of elk in the Muskwa in 1981–1989.

Cohort	Number of calves/100 females			
	5 months of age	9 months of age	17 months of age	21 months of age
1981	—	16.2 (961)	—	10.0 (259)
1982	—	13.2 (272)	—	13.1 (689)
1983	—	13.2 (734)	11.8 (389)	11.5 (712)
1984 R	39.4 (412)	37.3 (753)	36.3 (523)	20.9 (890)
1985 R	60.4 (618)	32.9 (983)	19.0 (1623)	18.2 (659)
1986	25.8 (1775)	22.2 (719)	23.7 (988)	24.4 (1178)
1987 R	49.3 (1105)	32.2 (1322)	—	19.2 (979)
1988	—	—	—	13.5 (591)
1989	—	22.3 (1631)	—	—

Note: GLM procedure: wolves reduced/not reduced, $F = 24.58$, $P = 0.0001$; age (5, 9, 17, 21 months), $F = 12.69$, $P = 0.0002$; cohorts, $F = 4.20$, $P = 0.054$; age \times wolves, $F = 5.60$, $P = 0.029$. "R" denotes a cohort in an area where wolves were reduced prior to parturition. Numbers in parentheses show the number of females.

tern; in the Kechika there were 3.4 packs/1000 km² before removal (March 1982), and in the following years, aggregation densities were 4.1, 3.4, 5.0, and 5.0/1000 km², and in 1987, following no removal in 1986, there were 3.6/1000 km².

Ungulate recruitment

The R value for young ungulates 5 and 9 months of age in the Kechika and Muskwa was negatively correlated with the density of wolves prior to parturition (Tables 3–5 and Fig. 5). Also, when the recruitment of moose and elk was regressed on the number of wolves per 100 moose or elk (an index to the numerical response of wolves), the regressions were curvilinear and negative with large r^2 values; the regression of the number of calves per 100 females for moose (Kechika and Muskwa) was $Y = 30.840X^{-0.748}$ ($r^2 = 0.685$, $n = 17$), and for elk in the Muskwa, $Y = 32.543X^{-0.540}$ ($r^2 = 0.576$, $n = 8$). The regressions of R on wolf numbers were generally curvilinear, which indicates that as mortality increased, it did so at a decreasing rate. Thus, when wolf numbers were reduced, the survival of young generally increased 2–5 times compared with control populations between areas within years for the Kechika and between years for the Muskwa (Tables 3–5).

There was no significant difference in the size of the moose cohorts between 5 and 9 months of age ($P = 0.938$) that would suggest differential mortality of recruits and adults after 5 months of age. However, the size of the new cohorts of sheep and elk continued to decrease between 9 and 21 months of age (Tables 3 and 4). The recruitment of caribou was measured primarily at 5 months of age, so we could not judge whether animals 5+ months of age were still more susceptible to greater mortality than adults; however, recent telemetric studies have shown that calves died over winter at higher rates than adults in two herds (Fancy et al. 1994; Boertje et al. 1995; see also Miller 1975).

When snow cover in the spring, prior to parturition in March + April + May or only in May, was incorporated as a variable with wolf density, there was little improvement in the variance in recruitment at 5–9 months of age that was explained by the combined factors r^2 (Table 6). Also, snow

cover prior to parturition as a single factor never explained a significant proportion of the annual variation in recruitment as wolf numbers did (Table 6).

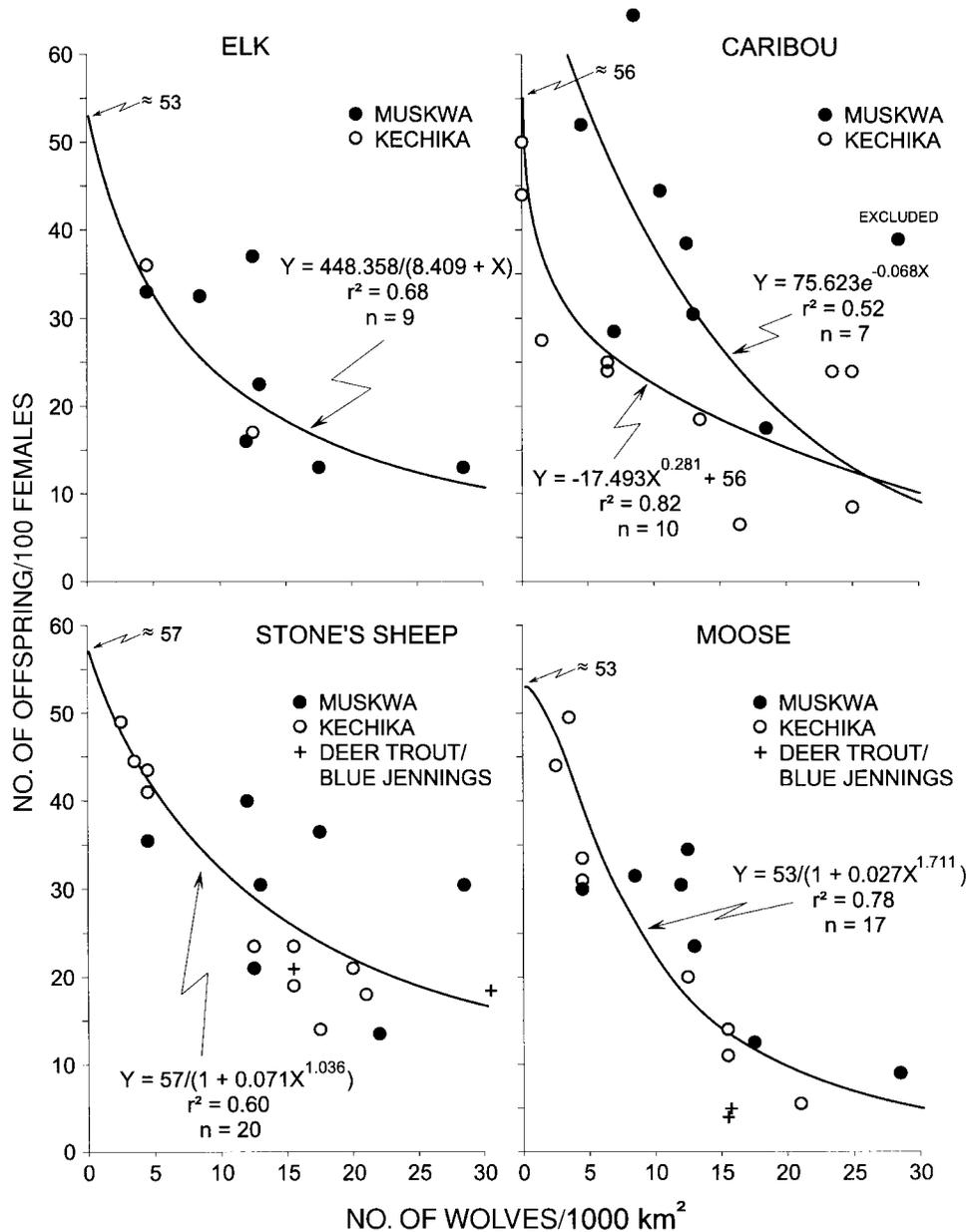
We assessed four hypotheses proposed to account for the continued decline in the calf cohorts of elk and sheep from 9 to 21 months of age (Table 7): (1) the classifications of yearling male elk and yearling ewes underestimated the size of these cohorts, (2) wolves continued to select yearlings over adults, (3) young animals died from starvation, and (4) wolves were more successful in killing young animals in deep snow. The classification technique may have underestimated yearling survival, but there were some years when there was no decline in the cohort representations for either elk or sheep (Tables 3 and 4). There was also great variability in the changes between ages within cohorts, suggesting that differential mortality did occur. Multiple regression and correlation analyses for the decline in sheep survival suggest that wolf numbers, not the severity of the winter (in either the first or second winter), explained the continued decline in recruitment of sheep 9–21 months of age (Table 7). But in the analysis of the continued decline in young elk 9–21 months of age, the factor that explained the greatest proportion of the variability was snow cover. The decline in elk calves between 9 and 21 months of age in the 1981 cohort could have resulted from starvation in the winter of 1981–1982, the most severe winter in 26 years (Fig. 2). These elk are living at the northern edge of their range in a snow shadow and have starved in the past (Peck 1980; Spalding 1992). The 1985 cohort showed a major loss also, but this occurred between 9 and 17 months of age, snows were deep in the winter of 1985–1986, and wolves had shown a major recovery from the reductions in 1985. This cohort may have been subject to surplus killing in deep snow, since the elk were aggregated in all years. In the census block with the highest density, there were 665 elk in 23 km² in 1982, 456 in 1985, and 637 in the same block in 1987.

Another interesting survival sequence for elk comprised a major loss of 46% between 5 and 9 months of age for the 1985 cohort, a small loss for the 1986 cohort from 5 to 21 months of age, and a major loss for the 1987 cohort between 9 and 21 months of age (Table 4). These trends suggest changes in vulnerability to predation. The 1985 cohort had high initial survival following the wolf reduction, even through their dams may have been stressed by the great snow depths in 1985; thus, there were still lots of calves as the wolf population rebuilt. For the 1986 cohort, early mortality must have been high without wolf reductions, probably exceeding 65%, and perhaps the vulnerable progeny had been culled early for that cohort. The 1987 cohort faced increased predation in 1988 after wolf numbers recovered. For elk, initial survival to 5 months of age was high because of reduced predation, but they appeared to be still more vulnerable to a wolf \times snow sequence until they reached adult size by 21+ months of age.

Population growth

The quadrat counts of moose in the Kechika in 1984 and 1988 gave a census (λ) value of 1.02 ($P = 0.210$). For the Muskwa, the λ value was 0.92 for the census of 1982 versus 1985 ($P = 0.220$) and 1.17 for 1985 versus 1989 ($P = 0.004$).

Fig. 5. Regressions of recruitment on wolf densities prior to birth for caribou at 5–9 months of age and sheep, moose, and elk at 9 months of age. Wolf densities $\leq 10/1000 \text{ km}^2$ resulted from wolf reductions in February–March, prior to the birth of the cohorts.



Again, in the Muskwa the λ values for the elk population were 0.96 for 1982 versus 1985 ($P = 0.482$) and 1.08 for 1985 versus 1989 ($P = 0.059$) (Table 8). A problem with most of the λ values is that they span a period of years that includes cohort additions before wolf reductions as well as cohort increments following reductions.

The complete counts of caribou and sheep in the Kechika indicate that populations generally increased when large recruitments were added after wolf reductions and decreased when smaller additions followed no wolf reductions. The mean λ values for caribou were 1.14 ± 0.061 ($n = 4$) after reductions and 0.93 ± 0.084 ($n = 4$) without reductions ($P = 0.039$) (Table 5). For sheep in the Kechika, based on subpopulations, the mean λ values were 1.08 ± 0.032 ($n =$

10) following wolf reductions and 0.89 ± 0.024 ($n = 13$) in the absence of removals ($P = 0.0001$).

Hunting success data for the Muskwa indicated no clear trends for moose, elk, or sheep prior to reductions (Table 9). After 1982, hunting success improved for moose and hunting effort improved for sheep, but elk statistics showed no trend (Table 9).

Hunting success data for the Kechika indicated a significant improvement in the number of days required to secure a moose or sheep after wolf populations were reduced (Table 9). Prior to reductions, the moose population in the Kechika was probably declining (Table 9). The Kechika sheep population showed no significant trend, based on hunting statistics prior to reductions, even though the census

Table 5. Population size of the Horse Ranch caribou herd in the Kechika, with recruitment at 5 months of age, and recruitment of caribou in the Muskwa.

Year	Kechika			Muskwa	
	Total census	No. of calves 5 months of age/100 females	Rate of increase	No. of calves/100 females	
				5 months of age	9 months of age
1977	237	10.0 ^a	—	—	—
1978	263	24.2	1.11	—	—
1979	374	25.1	1.04	—	45.7 (290) ^a
1980	311	27.3	1.14	—	28.4 (443) ^a
1981	329	18.4	1.06	—	—
1982	337	6.7	1.02	—	—
1983	250	8.4	0.74	39.1 (64) ^b	—
1984	209	24.3	0.84	—	—
1985	274	50.7	1.31	52.1 (96) ^b	38.6 (256) ^a
1986	—	24.0	—	—	—
1987	—	43.8	—	64.6 (113) ^b	30.4 (220) ^b
1988	—	—	—	—	—
1989	—	—	—	—	—
1990	—	—	—	—	17.5 (212) ^b

^aCows are not distinguished; assumed to be two-thirds of adults. Values in parentheses represent the total number of animals classified.

^bNumbers in parentheses show the sample size for cows.

data from the Kechika indicated a decline (Table 8). The indices supported an increase in moose and sheep in 1982–1988 but no obvious trend in 1976–1982.

The last index used to determine population trends was a comparison of observed R with R_s values. The mean R_s values for the four species, based on the regression of λ on R (Fig. 6 and data from Tables 3–5), were 19.0 for caribou ($n = 8$), 24.1 for sheep ($n = 17$), 24.9 for moose ($n = 3$), and 23.6 for elk ($n = 2$). We calculated the following values from the literature or our own files: $R_s = 22.1$ at 9 months of age for caribou in Pukaskwa National Park, Ontario ($n = 15$) (A.T. Bergerud, unpublished observations), $R_s = 25.6$ at 13 months of age for sheep in the Yukon ($n = 12$) (Hoefs and Cowan 1979; Hoefs and Bayer 1983), $R_s = 28.4$ at 9 months of age for moose in Pukaskwa National Park (not shown) (Bergerud et al. 1983), $R_s = 24.7$ at 9 months of age for moose on Isle Royale ($n = 19$) (Peterson 1977; Peterson and Page 1988), $R_s = 19.5$ at 17 months of age for moose in the Yukon ($n = 16$) (Larsen et al. 1989b), $R_s = 26.0$ at 17 months for moose in Alaska ($n = 16$) (Gasaway et al. 1992), and $R_s = 23.7$ at 6 months for elk in Riding Mountain National Park (Carbyn 1989; L.N. Carbyn, personal communication). The R_s value for the 11 data sets was 24.1 ± 0.91 (coefficient of variation (CV) = 12.5%). Also available in the literature was the percentage of caribou calves of the total number that yielded a λ value of 1.00, based on 32 herd determinations (Bergerud 1992) and the percentage of calves of the total number of animals that balanced mortality in 18 determinations for caribou (Bergerud and Elliott 1986). If the sex ratio for adults is considered to be 1 male to 2 females (Bergerud 1980), these percentages convert to 27.7 and 20.4 calves/100 females as estimates of R_s for caribou and represent the majority of the herds in North America.

The lack of variation in R_s values is, we believe, due to the little variation in the natural mortality rates of adult females of the four species when populations are stable. The natural mortality rates of females have commonly been reported to fluctuate in the range 9–15% for populations not in a major decline; hence, these mortality rates can be balanced by fairly constant recruitments. Annual mortality rates reported for ewes in North America range from 12 to 15% (Hoefs and Cowan 1979; Hoefs and Bayer 1983; Burles and Hoefs 1984; Simmons et al. 1984). Reported mortality rates for cow moose vary from 7 to 13% (Wolfe 1977; Gasaway et al. 1983; Boertje et al. 1988; Larsen et al. 1989a, 1989b). For caribou, rates again approximate 7–15% (Bergerud 1980, 1983; Hatler 1986; Hearn et al. 1990). The mortality rate for cow elk was 12% on Vancouver Island, B.C. (Brunt et al. 1989). The mortality rate for females of the four species in populations that were mostly stable was $11.6 \pm 0.87\%$ (CV = 29%, $n = 15$). Now, if 12% of the females die per year, ~24 new calves/100 females are required each year to balance these losses if the number of male recruits equals that of females.

The finding of similar mortality rates and R_s values for the four species is not surprising, since these species have similar life expectancies. The regressions of λ on the number of calves per 100 females (Fig. 6) indicate that the survival rates of calves and adults are positively correlated because of the common significance of predation. But these survival regressions have different slopes between the species and thus do not explain the constant R_s – adult mortality relationship.

In all years, following wolf reductions, recruitments were greater than ~24 offspring/100 females (Tables 3–5). In the absence of wolf reductions, $R < R_s$ for moose and elk in gen-

Table 6. Comparison of probabilities and r^2 values for wolves when recruitment is regressed on wolf numbers and snow statistics (WE, March, April) prior to parturition as single factors and combined in a multiple regression.

	Probability of no difference		r^2
	Wolves	Snow ^a	
Caribou 5 months of age			
Kechika ($n = 10$)			
Wolves	0.024	—	0.493
Snow	—	0.800	0.009
Wolves + snow	0.009	0.119	0.551
Sheep 9 months of age			
Kechika + Muskwa ($n = 19$)			
Wolves	0.0007	—	0.499
Snow	—	0.624	0.144
Wolves + snow	0.0003	0.109	0.553
Moose 5 months of age			
Kechika + Muskwa ($n = 14$)			
Wolves	0.0001	—	0.830
Snow	—	0.609	0.225
Wolves + snow	0.0001	0.459	0.809
Elk 5 months of age			
Muskwa ($n = 4$)			
Wolves	0.059	—	0.886
Snow	—	0.709	0.225
Wolves + snow	0.125	0.371	0.809
Elk 9 months of age			
Muskwa ($n = 7$)			
Wolves	0.024	—	0.493
Snow	—	0.800	0.009
Wolves + snow	0.049	0.181	0.545

^aUsing multiple regression for May snow only, $r^2 = 0.760$, $P = 0.106$ for snow alone.

eral, but $R \geq R_s$ for some cohorts of sheep, as well as three of four cohorts of caribou, in the Muskwa (Tables 3–5).

Discussion

Prior to the reductions in wolf numbers, the populations of all four ungulate species were either stable in numbers (no clear trend) or decreasing (Tables 8 and 9; Bergerud and Elliott 1996). After the reductions in the wolves, all the ungulate populations increased (Tables 5, 8, and 9). Predation by wolves was a major factor limiting population growth.

Two hypotheses proposed to explain the regulation of wolf numbers are (1) that wolves self-regulate through territorial behaviour (Mech 1966; Haber 1977; Packard and Mech 1980, 1983) and (2) that wolves adjust their numbers on the basis of prey biomass (Van Ballenberghe et al. 1975; Keith 1983; Fuller 1989). The results of this study and that of Bergerud and Elliott (1986) support the second hypothe-

sis. In the former study we reported a density of 0.3 moose/km² and 0.06 caribou/km² in the Horseranch Mountains; this translates to a predicted wolf density of 10.4/1000 km², based on biomass (Fuller 1989), and the observed density before removals was 10.0 wolves/1000 km² in 1978 and 9.7 wolves/1000 km² in 1982, 2 years after the removals (Bergerud and Elliott 1986). In this study in the Kechika prior to removal in 1982 there were an estimated 10 000 moose, 3500 sheep, and 500 caribou. These prey numbers, based on Fuller's regression of wolf numbers on prey biomass for 25 studies across North America, should support 15.9 wolves/1000 km², and the 1982 census prior to removal gave 15.5 wolves/1000 km². Again in the Nelson region our very extensive census (10% of the area) gave 0.08 moose/km² and 4.1 wolves/1000 km², and the predicted wolf density from Fuller's regression was 5.2 wolves/1000 km². A 10% correction for overlooked singletons (Boertje et al. 1996) would reduce the difference between observed and expected numbers. Each year after we removed wolves, large numbers of wolves repopulated, the densities approaching preremoval numbers and the number of aggregations in the core removal area in the Kechika being quite constant and similar to that before removal.

In the Muskwa the density of wolves in 1978–1980 was <10/1000 km², well below the 29 wolves/1000 km² predicted from the prey-biomass censuses of moose and elk in 1982 (caribou and sheep densities are based on the 1990 census). This wolf population, when released from the scattered control by outfitters, increased to nearly 40/1000 km² by 1984, exceeding the biomass prediction, at least temporarily. These results are not consistent with the paradigm of territorial self-regulation or with the concept of the prudent predator (Slobodkin 1968, 1974). The recolonization data in both areas support Fuller's (1989) view that dispersal is a primary mechanism in the adjustment of wolf numbers according to prey abundance, and presumably results in increased survival.

Bergerud (1992) has argued that the dynamics of wolf × prey systems should not be modelled after the extensive studies of wolves on Isle Royale, as a number of workers have done, since the surrounding water is a barrier to ingress and egress, preventing adjustments to changes in prey abundance. In such a saturated insular population, in contrast to noninsular systems, social self-regulation may well be the major force in the stability of wolf numbers and their slow response to changes in prey biomass (Mech 1966; Peterson 1977; Peterson and Page 1988).

There is a great deal of public concern about the management and conservation of wolf numbers by means of removal programs. We removed 505 wolves from the Muskwa and the numbers of moose and elk increased by 10 000 animals (20 per wolf removed); we argue cause and effect. In 1989, after the removals the prey biomass was sufficient to temporarily support 40 wolves/1000 km² (750 wolves) (although the most numerous ungulates would decline; Tables 3 and 4), whereas in 1982 the prey base was available for 29 wolves/1000 km² (550 wolves). With predator/prey management a greater biomass of ungulates and wolves can be predicted than in a laissez-faire system (Boertje et al. 1996). By 1989, this management effort had resulted in the greatest biomass of ungulates coexisting with wolves and

Table 7. The decline in recruitment of elk and sheep in the Muskwa between 9 and 21 months of age, with wolf numbers and snow statistics.

Year of birth	Difference in no. of offspring 9 and 21 months of age/100 females		No. of wolves/1000 km ² in March when young were 10 months of age	Water equivalent ^a
	Elk	Sheep		
1981	-6.2	-21.4	17.7	578
1982	-0.1	-23.1	28.7	254
1983	-1.7	-3.7	12.3	180
1984	-16.4	0 ^b	4.3	547
1985	-14.7	-18.4	12.9	395
1986	0	0	8.5	185
1987	-13.0	—	Increasing ^c	133

^aSnow statistics for March + April + May; animals were 10–12 months of age.

^bValue at 21 months of age \geq value at 9 months of age.

^cDensity of wolves in March 1990 was 22/1000 km². Correlation coefficient: elk and wolves, $r = -0.501$, $P = 0.311$; elk and snow water equivalent, $r = 0.726$, $P = 0.103$; sheep and wolves, $r = 0.833$, $P = 0.039$; sheep and snow water equivalent, $r = 0.249$, $P = 0.635$. Multiple regression: difference = wolves (W) + snow water equivalent (S): sheep, $Y = -14.480 + 1.177W + 0.025S$; wolves, $P = 0.027$; snow water equivalent, $P = 0.163$; elk, $Y = -1.505 - 0.335W + 0.027S$; wolves, $P = 0.337$; snow water equivalent, $P = 0.146$.

Table 8. Census results and estimated total numbers of ungulates in the study areas.

Species and area	Year of census	Area censused (km ²)	Density (no./km ²)		Estimated population	Rate of increase
			Census area	Total region		
Moose						
Muskwa	1982	183 ^a	0.97	0.97	18 500	—
	1985	183 ^a	0.77	0.77	14 600	0.92
	1989	183 ^a	1.41	1.41	26 800	1.17
Kechika	1984	108 ^a	0.86	0.53	9 800	—
	1988	108 ^a	0.94	0.58	10 700	1.02
Nelson	1988	2151 ^a	0.076	0.076	1 600	—
Elk						
Muskwa	1982	183 ^a	7.01	0.22	4 200	—
	1985	183 ^a	6.13	0.24	4 600	0.96
	1989	183 ^a	8.54	0.33	6 300	1.08
Sheep						
Kechika	1977	1420 ^b	0.58	0.16	2 900	—
	1981	2355 ^b	0.49	0.14	2 500	0.96
	1983	3432 ^b	0.39	0.11	1 950	0.89
	1984	2082 ^b	0.41	0.11	2 050	1.05
	1985	3275 ^b	0.35	0.10	1 750	0.85
	1986	4447 ^b	0.44	0.12	2 200	1.25
	1987	2162 ^b	0.56	0.15	2 800	1.27
Muskwa	1990	$\pm 4000^b$	0.30	0.16	3 000	—
Caribou						
Muskwa	1990	$\pm 4000^b$	0.30	0.16	3 000	—

^aStratified random census.

^bComplete count.

bears that had so far been reported in North America (Fuller 1989); this, we believe, was a plus for man and wolves alike, as well as a demonstration of the value of leaving land free of economic development. This area (Muskwa plus Kechika) has now been made a provincial park. But if the goal is to have large numbers of ungulates and wolves available for viewing, wolf management will be needed. Leaving parks unmanaged, like Denali National Park in Alaska and

Spatsizi in British Columbia, for example, can result in low numbers of ungulates and wolves.

Wolves have recently been introduced into the multiple-ungulate system in Yellowstone National Park. There was considerable disagreement between 15 wolf/ungulate experts on the impact of the introduction to Yellowstone on the population dynamics of the indigenous ungulates (Lime et al. 1993). There are eight ungulate species in Yellowstone and

Table 9. Regression and correlation statistics of hunting success and days needed to secure an animal in 1 year compared between seasons before wolf reductions in 1976–1982^a and after reductions in 1982–1988.

Area, species, and hunting statistics	Slope coefficient		<i>r</i>		Probability	
	Before	After	Before	After	Before	After
Muskwa						
Moose						
Days	-0.036	-0.625	-0.045	-0.564	0.92	0.18
Success	+0.304	+2.571	+0.203	+0.787	0.66	0.04
Elk						
Days	-0.643	+2.358	-0.283	+0.463	0.54	0.30
Success	+0.393	-0.536	+0.102	-0.200	0.83	0.67
Sheep						
Days	-1.014	-2.482	-0.249	-0.856	0.63	0.01
Success	+0.971	+0.946	+0.273	+0.626	0.60	0.13
Kechika						
Moose						
Days	+1.857	-2.143	0.664	-0.881	0.10	0.01
Success	-5.929	+5.107	-0.836	+0.853	0.02	0.01
Sheep						
Days	+1.146	-6.000	+0.229	-0.796	0.62	0.03
Success	+0.321	+4.964	+0.088	+0.827	0.86	0.02

Note: 1982 was used both before and after wolf reductions.

seven in the Muskwa, and both systems have brown bears, hence our results may have some relevance. Boyce (1993) modelled the potential impact of the introducing wolves to Yellowstone on the ungulates and predicted a population of 78 wolves in nine territories of the Park. This density of only 9 wolves/1000 km² would not result in $R < R_s$, based on our results. But Boyce's projection was based on the winter distribution of ungulates in only 820 km², or 10% of the Park. We believe the projected number of wolves for the Park should have been based on the densities of the four important biomass ungulate species (elk, deer, moose, and bison) as calculated using the prey biomass equation of Fuller (1989). When this is done on the basis of the ungulate numbers present in the Park and surrounding region (Singer and Mack 1993), the projected density of wolves for the Park is 43/1000 km², or when ungulate migrations are taken into account, >20 wolves/1000 km² for Yellowstone and the surrounding wilderness (ungulate numbers are taken from Singer and Mack 1993, Table 10, p. 97). Again, if that system is modelled after Walters et al. (1981), who regressed the territory sizes of wolves on prey biomass from seven studies, the projected wolf population still exceeds Boyce's estimate by a wide margin.

Our results suggest that the preparturient ranges of wolves and ungulates and the survival of young of the year (R) should be the focus of impact projections, rather than the winter locations of ungulates and the rates at which adults are killed. The Yellowstone system is an insular situation, but initially it would be nonsaturated and wolf numbers should expand as in the Muskwa and reach limits at or above that dictated by the prey biomass. Thus, our prediction is that wolves will exceed the R_s value for moose and elk by a significant margin, resulting in substantial declines.

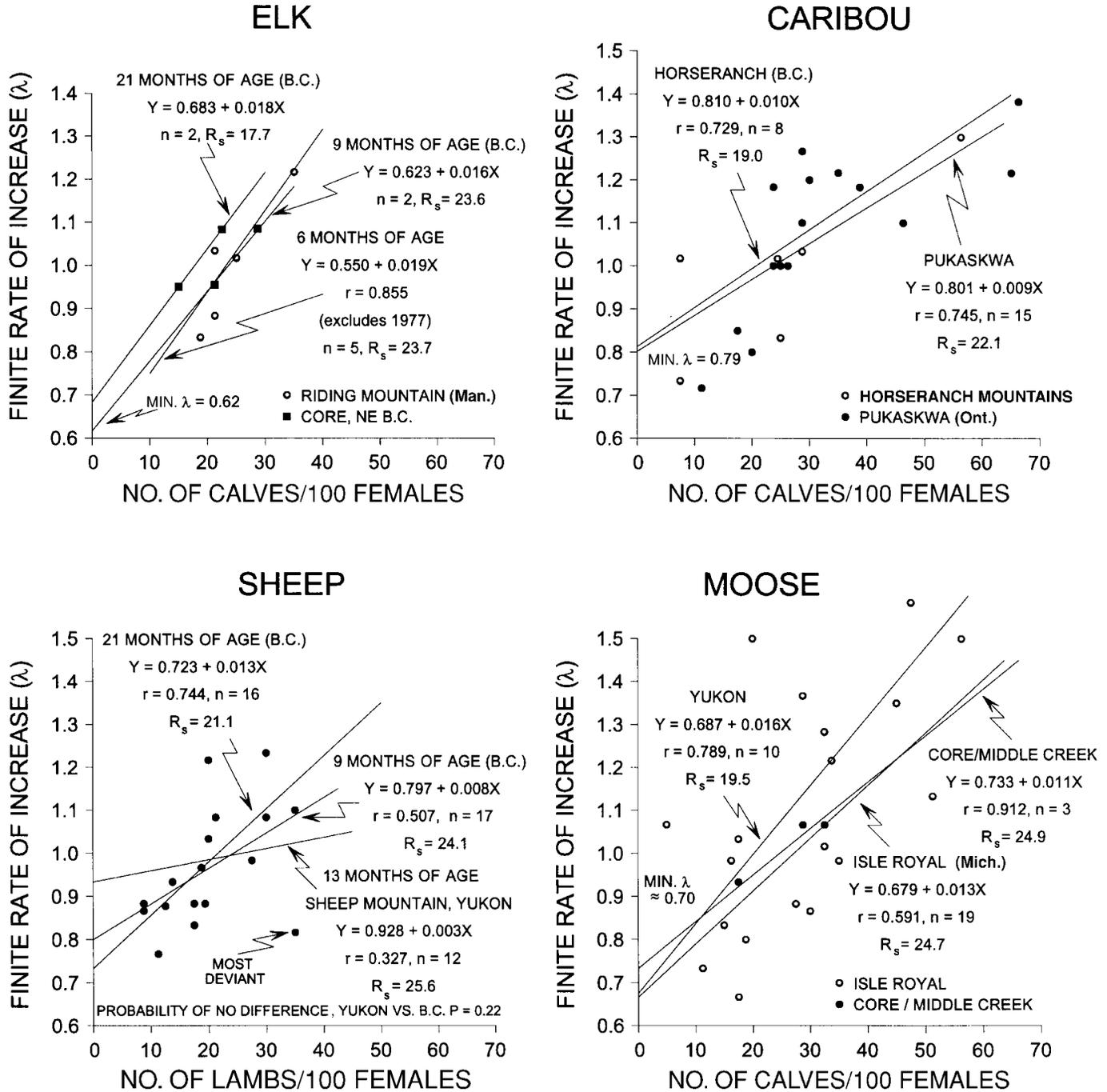
A major factor that has complicated our understanding of wolf predation on young ungulates in Alaska and Canada is the significance and confounding influence of bear predation

(for review see Ballard and Larsen 1987). The consensus is that bear predation is largely density-independent (Crête and Jolicoeur 1987; Boertje et al. 1988; Schwartz and Franzmann 1989). If this conclusion is valid, then bear predation and wolf predation are additive and bear predation would not have masked the curvilinear response of calf survival regressed against wolf numbers that we have presented.

In our multiple-ungulate system the regressions of R on wolf numbers intercepted the y axis of zero wolf numbers at 53–57 calves/100 females for all four species (but not caribou in the Muskwa) (Fig. 5) Yet the reported parturition rates of the four species vary widely: moose in our area gave birth to 112 calves/100 females (Larsen et al. 1989a; K. Childs, personal communication), caribou gave birth to 84 calves/100 females (Bergerud and Elliott 1986), elk gave birth to approximately 80 calves/100 females (Bunnell 1987; Brunt et al. 1989), and sheep produced even fewer, 70–75 lambs/100 ewes (Woodgerd 1964; Hoefs and Cowan 1979; Simmons et al. 1984). The difference between the birth rates and the survival estimates at 9 months, based on zero wolf abundance (the y intercept of wolf numbers regressed on prey biomass), may be useful as an index of the relative importance of bear predation on neonates between the species; this unexplained difference was 59 calves for moose, 27–28 calves for elk and caribou, and only 13 lambs for sheep, or a relative index of bear predation would be moose > caribou = elk > sheep.

This ranking is consistent with the literature, which shows that moose are heavily preyed on by bears (Ballard et al. 1987; for review see Ballard and Larsen 1987; Boertje et al. 1988; Larsen et al. 1989a; Ballard and Miller 1990). Bears also take caribou calves (Page 1988; Adams et al. 1995a, 1995b) and elk calves (Schlegel 1976), but there are no statements in the literature beyond anecdotal accounts of bears killing the lambs of Dall (*Ovis dalli*) or Stone's sheep

Fig. 6. Regressions of the finite rate of increase against recruitment for ungulate populations in northern British Columbia, including regressions for North American populations outside British Columbia where the ungulates had been censused and recruitment measured and annual harvests were $\leq 5\%$. These latter regressions are from the following sources: A.T. Bergerud, unpublished data; Peterson (1977); Hoefs and Cowan (1979); Hoefs and Bayer (1983); Bergerud et al. (1983); Burles and Hoefs (1984); Carbyn (1988); L.N. Carbyn, personal communication; Peterson and Page (1988); Larsen et al. (1989b); and Gasaway et al. (1992).



(see Murie 1944). It seems unlikely that bears would be sufficiently agile to capture lambs on cliff faces or in broken escape cover.

If there is a difference in the vulnerability of the four species to bear predation, it may be a factor in the difference between the species in the wolf densities needed to stabilize R . For moose, which are highly susceptible to bears, R was stabilized at only 9 wolves/1000 km², whereas for sheep, possibly not

as susceptible to bear predation, 15–17 wolves/1000 km² were required to stabilize R .

Keith (1983) and Fuller (1989) have reviewed the close correlation between wolf density and the combined biomass abundance of ungulates in various predator-prey systems in North America where both wolves and ungulates had been counted ($r = 0.85$ for 25 studies in Fuller 1989). Moose, because of their great biomass, make the largest contribution to

maintaining wolf numbers in most multiple-ungulate systems. The density of sheep in our study area at this time is less than $<0.20/\text{km}^2$ (caribou are also at this low density). At the end of the Little Ice Age in North America, ca. 1860, there were few, if any, moose or elk in our study area (Hatler 1950; Spalding 1990, 1992). Hence, it is possible that sheep densities in our areas in the past, prior to ingress by moose and elk, were much higher than at present. In this historically two-species system of sheep and caribou in northern British Columbia, both species could double their current densities in the Muskwa and there would still be only 8 wolves/1000 km^2 (Fuller 1989), sufficient for R_s for caribou and $>R_s$ for sheep. It is the addition of moose and (or) elk, the two ungulate species with high biomass, to the system that has allowed wolves to reach higher densities, sufficient that the spacing needed to maintain viable numbers of sheep and caribou in undisturbed systems will be $<0.25/\text{km}^2$ (Bergerud and Elliott 1986).

Central to this prey-biomass argument is the assumption that R_s remains unchanged with the addition of alternative prey, regardless of whether they divert or exacerbate predation on the primary prey. This held true for elk in our area versus Riding Mountain National Park (no caribou), for moose in our area versus Isle Royal (no caribou, sheep, or elk), for sheep in our area versus Sheep Mountain (no elk), and for caribou in our area (Horseshoe Mountains) versus Pukaskwa (no sheep) (Fig. 6). Caribou in North America have similar R_s values with and without moose as alternative/primary prey (Bergerud 1974).

A present-day example of this biomass interaction between ungulate species and wolf numbers is the system in west-central Yukon. In this system there were 0.06 moose/ km^2 , 0.010 caribou/ km^2 , and 0.68 Dall sheep/ km^2 (Sumanik 1987). The predicted wolf density based on ungulate biomass is 7.4/1000 km^2 (Fuller 1989) and the observed wolf density was 7/1000 km^2 (Sumanik 1987). In the presence of the small wolf population (8/1000 km^2 fewer than the stabilizing wolf density in our multiple-ungulate system), the sheep have had a positive R value ($>R_s$); with such a high density of 0.68/ km^2 , the sheep appeared to be limited by a forage \times snow interaction (Hoefs and Cowan 1979; Hoefs and Bayer 1983; Sumanik 1987). Now, we predict that if the moose population suddenly increased in this Yukon system so that there were >15 wolves/1000 km^2 , sheep would be kept at a lower density by predation rather than by a food \times snow interaction.

Our data suggest the hypothesis that as ungulate diversity and biomass increase, the ungulate \times wolf interaction becomes more unstable. In the Muskwa in 1984, the wolf density (39/1000 km^2) exceeded that predicted by the prey biomass of 28 wolves/1000 km^2 by 40%, and exceeded the wolf density that provided the mean R_s values (11/1000 km^2) for the four species by 250%. Again, in 1989 the wolf numbers projected on the basis of biomass were 28/1000 km^2 greater than the numbers that produced stable recruitment. For the less diverse Kechika system, the predicted wolf numbers based on biomass were 15.9/1000 km^2 in 1982 and 17.0/1000 km^2 in 1988, i.e., wolf numbers were only about 5/1000 km^2 above the density needed for R_s . In the simple Nelson system, there were far fewer wolves than the predicted numbers needed for stability in the Kechika and

Muskwa, yet the recruitment of moose in 1988 was 25 calves/100 females ($n = 88$ females) and 17% caribou calves ($n = 41$); in both cases recruitments were sufficient for stability (Bergerud 1992). The hunting returns from 1976 to 1988 for the Nelson indicated a stable population, based on hunter success and number of days needed to kill an animal. At low moose densities, 0.20–0.50/ km^2 (Bergerud 1992) or below 0.65/ km^2 (Messier 1994), wolf predation should be strongly density-dependent and maintain moose populations at low equilibrium densities for extended periods (Gasaway et al. 1992). Thus, in northeastern British Columbia, stability in wolf numbers was inverse to diversity and biomass: Muskwa $<$ Kechika $<$ Nelson.

The data presented by Fuller (1989) support the view that prey diversity destabilizes wolf numbers. His data show that percent deviation (\pm) of observed wolf numbers from expected numbers based on the regression line $Y = 3.4 + 3.7X$ ($n = 25$) increased with species diversity: $8.8 \pm 2.09\%$ for 1 ungulate species ($n = 6$ studies); $21.8 \pm 4.24\%$ for 2 ungulate species ($n = 12$); 32.5 ± 10.73 for 3 ungulate species ($n = 4$); and 41% for >3 ungulate species ($n = 1$) (two strongly deviant studies are excluded). Dale et al. (1995) showed that the accuracy of predictions of wolf numbers based on prey biomass, and also using data from Fuller (1989), could be enhanced if only the primary species were used in the predictions. Increased ungulate diversity appears to decrease the “fine tuning” of wolf numbers relative to prey abundance, leading to greater instability, contrary to classical ecological theory.

In our study, all four species decreased in numbers when wolf numbers were high and recruitment was low. The negative regressions of offspring survival on wolf numbers meant that the functional predation response (number of kills per wolf) decreased as the numerical response increased. Since wolf numbers and prey numbers in North America are positively correlated, these regressions suggest an inverse density dependence of offspring survival of the primary prey on predation. However, even with the maximum number of 39 wolves/1000 km^2 in the Muskwa in 1984, the expected numbers of offspring 9 months of age per 100 females were 3.3 for moose, 6.7 for caribou, 9.3 for elk, and 12.7 for sheep. Some young always survived.

We hypothesize that these curvilinear and concave regressions of survival result because preparturient females disperse in the spring (Geist 1971; Bergerud et al. 1984; McCullough 1985; Bergerud and Page 1987). At this spacing the moose would be in the most predictable locations at lower elevations, and the sheep possibly in the most inaccessible habitats. Further, many females show a high degree of philopatry and return each spring to the same general area to give birth (Geist 1971; McCullough 1985; Hatler 1986; Edmonds 1988). This maximum spacing and fidelity mean that the occupied range remains constant even when wolf numbers are high and many young are found by wolves. But as young are killed, the density of the remaining animals decreases, which increases the searching time per successful encounter and reduces the functional predation response (Bergerud and Page 1987).

The density-dependent-spacing hypothesis and the $>$ biomass diversity $>$ instability hypothesis were partially tested when Elliott recensused three populations in the Kechika in

1997 (sheep, caribou, and moose) and the moose population in the Muskwa in 1993. Wolf management had been laissez-faire in the Kechika since 1985 (12 years) and in the Muskwa since 1987 (6 years) (Elliott 1997). The moose population in the Kechika in 1997 had declined by 51% ($\lambda = 0.94$) since 1988 and moose numbers in the Muskwa core in 1993 were down by 53% ($\lambda = 0.83$) from 1989, and wolf numbers would have followed. But the low-density sheep and caribou populations in the Kechika had maintained their numbers and the caribou were more widely spaced in 1997 than previously (Elliott 1997). These findings are consistent with reduced predation of widely spaced versus closely spaced ungulates, and with wolf \times ungulate interactions being more unstable in the Muskwa, with its higher biomass and diversity, than in the Kechika.

The coexistence of species is a central problem of ecology, and the continued existence of ungulates limited by effective predation is of theoretical interest. For deer, sheep, moose, elk, and sedentary caribou in North America, a generalization is that they aggregate on lowlands in the winter. In the spring, sexual segregation results when females leave winter ranges before males (Leopold et al. 1951; Geist 1971, 1982; Bergerud et al. 1984); the females disperse as they migrate, those in some populations seeking higher elevations even when plant phenology is delayed (Geist 1971; Bergerud et al. 1984, 1988, 1990; Ferguson et al. 1988; Cichowski 1989; for review see Main and Coblenz 1990; Seip 1992). We suggest that this spacing out in the spring by females is an ultimate response at the individual level to the need to reduce the predation risk for neonates; at the population level this antipredator strategy is a major density-dependent damping mechanism that reduces the possibility of extinction.

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