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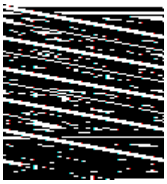

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SPECIES-SPECIFIC POPULATION DYNAMICS OF CERVIDS IN A MULTIPREDATOR ECOSYSTEM

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Abstract: In response to the natural experiment created by gray wolf (*Canis lupus*) recolonization of the Glacier National Park area, from 1990 to 1996 we examined population trends and female survival rates of white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and moose (*Alces alces*) preyed upon by wolves, cougars (*Puma concolor*), bears (*Ursus* spp.), coyotes (*Canis latrans*), and humans. The effects of the complete suite of native large carnivores on prey have not been previously reported. Annual survival rates were 0.74 for 64 deer, 0.83 for 53 elk, and 0.88 for 47 moose. Cougars and wolves were the most significant sources of mortality for deer (0.09 and 0.06 respective annual cause-specific mortality rates) and elk (0.06 and 0.03 respective annual cause-specific mortality rates), and wolves and bears were the most significant sources of mortality for moose (0.03 and 0.04 respective annual cause-specific mortality rates). All age classes of deer were relatively equally vulnerable to predators, while young and old moose and elk were most vulnerable. Moose survival rates were higher where wolves were absent and where white-tailed deer were present. Deer and elk populations declined as wolf numbers increased ($\lambda = 1.20$). The moose population remained relatively stable. Predation appeared to be the primary factor limiting growth of deer and elk populations in this system. Predator–prey managers need to carefully monitor prey populations in areas wolves recolonize. Managers may be able to manipulate alternative prey densities to enhance prey populations that are affected by wolves, cougars, and bears.

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Key words: *Alces alces*, *Canis lupus*, cougar, elk, gray wolf, grizzly bear, moose, *Odocoileus virginianus*, predator–prey, *Puma concolor*, *Ursus arctos*, white-tailed deer.

Recent emphasis in ecology and conservation biology has shifted from single-species management to multispecies and ecosystem management, but few studies in North America have investigated predation in areas of high diversity of large predators and prey (Huggard 1993, Boyd et al. 1994, Weaver 1994). Those studies, however, have focused on the predator side of the relationship and on only 1 predator. Little work has been done to simultaneously and directly examine how prey cope with >1 predator.

The natural experiment created by wolf recolonization of northwestern Montana in the mid-1980s (Ream et al. 1989) produced a great opportunity to elucidate predator–prey relationships in a complex predator–prey ecosystem in and near Glacier National Park. Until the restoration of wolves into Yellowstone National Park in 1995, northwestern Montana was the only area in the United States where the 3 top-level North American predators, wolves, cougars, and grizzly bears (*Ursus arctos*), coexisted. The potential for such an assemblage of predators to affect prey populations is substantial (Messier 1994), and the effects of predators on prey populations was among the greatest concerns of the public regarding wolf recovery in the northwestern United States (U.S. Fish and Wildlife Service 1987, 1994).

We examined predator–prey relationships between large carnivores, white-tailed deer (hereafter, deer), elk, and moose in the North Fork of the Flathead Valley (North Fork) in northwestern Montana and southeastern British Columbia from 1990 through 1996. Our objectives were to determine (1) the causes, extent, and timing of mortality in females of each species; (2) factors affecting the relative vulnerability of each species to specific predators; (3) population trends of each species; and (4) the effect of predators on population trends. We also examined the effects of wolf and deer presence on relative survival rates of cervids. Finally, we examined the role of environmental and animal condition parameters in prey to assess the role of these factors relative to the role of predators in affecting population trends of cervids.

We hypothesized that predation would be-

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come the primary factor limiting growth of cervid populations concurrent with wolf recolonization in our study area. We use the term "limiting factor" as I that far outweighs others in impeding the rate of increase (Leopold 1933: 39). We examined limiting factors to estimate the relative contribution of each to the trend in cervid populations and to identify the conditions leading to limitation (Messier 1991, Van Ballenberghe and Ballard 1994). We derived a set of predictions to test the validity of the hypothesis: (1) predators should be the primary cause of mortality in cervids; (2) predator-caused mortality should be mostly additive (e.g. predators do not kill only age classes that are most likely to otherwise die from other causes; (3) kill rates of each species of predator should be additive to each other, to other sources of mortality, or both; (4) predator density should explain more of the variation in cervid population trends than snow depth or animal condition; and (5) relative to other areas in the region with lower densities of predators, hunter success for cervids in the North Fork should be lower and cervids should have higher rates of survival and be in better nutritional condition (due to their lower density).

STUDY AREA

The Whitefish and MacDonald divides formed the western border of the North Fork study area, and the Livingstone Range and Continental Divide formed the eastern border. The valley bottom varied from 4 to 10 km in width and rose from 1,024 m elevation in the south to 1,375 m in the north. Land east of the North Fork River and south of British Columbia fell within Glacier National Park (GNP). West of the river, land ownership was a mosaic of Flathead National Forest, Coal Creek State Forest, and private property. The density of humans was <0.005/km^2 in British Columbia and <0.1/km^2 in Montana.

The climate is transitional between northern Pacific coastal and continental. Mean temperatures ranged from −9°C in January to 16°C in July (Singer 1979). Snow normally covered the area from mid-November through mid-April. The annual maximum snow depth at the Polebridge Ranger Station averaged 65 cm. Dense lodgepole pine (*Pinus contorta*) forests dominated most of the valley, but sub-alpine fir (*Abies lasiocarpa*), spruce (*Picea* spp.), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*) communities existed throughout the valley. Abundant meadows and riparian areas were dispersed throughout the study area. Detailed descriptions of vegetation communities in this area were provided by Jenkins (1985) and Krahmer (1989).

Approximately 10 wolves/1,000 km^2 (Pletscher et al. 1997) and 70 cougars/1,000 km^2 (winter density estimate within a subportion of the study area; T. K. Ruth, Hornocker Wildlife Research Institute, personal communication) inhabit the study area. Grizzly bear density was estimated to be 64 bears/1,000 km^2 for the Canadian portion of the study area (McLellan 1989), and black bear (*Ursus americanus*) density estimated to be approximately 200 bears/1,000 km^2 (B. N. McLellan, British Columbia Ministry of Forests, personal communication).

METHODS

Survival Rates (Predictions 1, 2, 3, and 5)

Cervid Trapping and Mortalities.—During winter 1990–95, we captured deer in traps (Clover 1956) on 3 winter ranges in GNP, and elk in collapsible traps (Clover 1956) in the Big Prairie grassland in GNP and along the North Fork River bottom. We captured moose by using darts filled with 3.9 mg Carfentanil (Meuleman et al. 1984) and 0.25 mg Rompun fired from a helicopter in January and December 1990. Carfentanil was reversed with 6 cc of Naltrexone. Moose were net-gunned from a helicopter in December 1993. We fitted females of all 3 species with radiotransmitters containing mortality sensors, and we pulled a lower canine tooth for aging (Gilbert 1966). We followed protocols approved by the University of Montana Animal Care and Use Committee.

We monitored radiotagged deer, elk, and moose for mortality signals at least 2–3 times/week during winter and spring and 1–2 times/week during summer and fall. When a mortality signal was received (usually 1–4 days after death), the radiocollar was located and the site and any remains were examined to determine cause of death. Predation was considered the cause of death when blood, subcutaneous hemorrhaging at wound sites, or signs of a struggle were found at the site. Tracks, scats, hair, and disposition of the carcass were used as evidence to determine the species of predator responsible (O'Gara 1978). We classified the cause of mortality to a dual predator group when evi-

dence of 2 predators was found and we could not determine which predator had made the kill.

We computed survival and cause-specific mortality rates via the program MICROMORT (Heisey 1985, Heisey and Fuller 1985); the biological year began on 1 June, the assumed birthdate of fawns and calves. Initially, each month was considered an interval with a constant daily survival rate. Daily survival rates for each interval were compared by log-likelihood ratio analysis; data from intervals were pooled if rates were not significantly different (Heisey and Fuller 1985).

Signal loss from radiocollars after the expected 2-year life of the battery was assumed to result from battery failure. We also assumed battery failure in 1 radiocollar on a deer that disappeared after only 160 days, because the pulse rate of the transmitter doubled shortly after it was placed on the deer. Mortalities that occurred within 12 days of capture were assumed to be capture-related and were not included in survival rate calculations (Harthoorn 1977).

Effect of Age on Survival.—We separated radiotagged animals into classes to compare their respective survival rates with *Z*-tests (Heisey and Fuller 1985). Deer were pooled into age classes by 2-year intervals. Elk and moose were pooled into 3 age classes because of smaller sample sizes.

Effect of Wolf and Alternative Prey Density on Survival.—We used *Z*-tests to compare survival rates of deer, elk, and moose among areas differing by the presence of wolves and the presence of deer. Wolf presence was known because all wolf packs within the study area contained radiotagged wolves that were tracked regularly through the duration of our study (Pletscher et al. 1997).

Recruitment Rates (Prediction 4)

Deer.—We counted male, female, and fawn deer in open fields on approximately 10 evenings in late April and early May each year to estimate fawn:doe ratios and classify deer by sex. We drove a 13-km transect beginning 1 hr before sunset and counted and classified deer through a spotting scope. We also estimated fawn:doe ratios by approaching radiotagged does in late April and early May each year until we could confirm the number of fawns with each doe.

Elk.—Elk were counted and classified by sex and age from a Cessna 182 along a survey route that was flown 5 times in January of 1991 and 1992 (Bureau 1992). A helicopter survey was flown each April from 1993 to 1996. For the latter survey, the study area was stratified into low-, medium-, and high-density subunits. All elk visible to the pilot and 2 observers were counted and classified by sex and age in a sample of these subunits each year. Sightability corrections and population estimates were computed via the computer program AERIAL SURVEY (J. W. Unsworth et al. 1991. Aerial survey: user's manual, unpublished. Idaho Department of Fish and Game, Boise, Idaho, USA.). Mean elk population estimates were compared between years via 2-sample *t*-tests. Probability values used for determining significance were adjusted by multiplying by the number of comparisons (Bonferroni adjustment [e.g., $P = 0.01$ and comparisons = 3; $0.01 \times 3 = 0.03$; Rice 1989]).

Moose.—In 1993–96, we located all radiotagged moose on 3–5 flights each April with a Cessna 185 to determine the number of calves with each cow. Only those moose for which we were confident about the presence or absence of a calf or calves were used in estimating the calf:cow ratio.

We estimated finite rate of change (λ) for populations of female deer, elk, and moose following Hatter and Bergerud (1991):

$$\lambda = (S)(1 - R),$$

where S = the finite annual adult survival rate; and R = the finite annual recruitment rate = $(Y2)/(100 + Y2)$, where Y = the number of young/100 females. We derived confidence intervals for λ by using the upper and lower limits of confidence intervals computed for survival rates by MICROMORT and confidence intervals computed for fawn:doe and calf:cow ratios (from AERIAL SURVEY) in the λ equation. We had no estimate of variance from our moose calf:cow surveys, so we could not estimate confidence intervals for moose λ.

Pellet Trend (Prediction 4)

We counted deer and elk pellet groups in 80 uncleared 1.8-m-radius plots on each of 11–17 pairs of transects during late April and early May each year. Using power analysis, Rachael (1992) indicated that 438 plots/year would be sufficient to detect a 20% change in population with 90% certainty. Plots were spaced at 50-m

intervals along the transect (40 plots/transect), and paired transects were spaced 200 m apart at 1.6-km intervals along Glacier Route 7. Transects were distributed to encompass the entire range of habitat types and geographic variation in the area. Because pellet data were not normally distributed, we used the Kruskal-Wallis test to compare mean number of pellet groups per plot among years. When Kruskal-Wallis tests were significant, we used the Newman-Keuls multiple comparison test to determine where differences occurred between years.

Hunter Success (Predictions 4 and 5)

We assisted Montana Fish, Wildlife and Parks in operating a hunter check station each year to estimate condition, age, and sex of hunter-killed deer and elk and to estimate hunter effort and success. Annual data were compared among years and to other check stations in the region. Densities of wolves in all other areas were significantly lower than the North Fork (U.S. Fish and Wildlife Service 1996). We estimated condition of deer via diastema lengths of yearling males killed by hunters, and we used correlation analysis to estimate trend (Reimers 1972, Frisina and Douglass 1999). We compared mean diastema length of yearling male deer with other hunting units in northwestern Montana by 1-way analysis of variance (ANOVA) and Duncan's multiple-range post hoc tests. We correlated hunter days per deer or elk harvested in the North Fork and in other hunting units in the northwestern region of Montana with year to estimate the trend in the deer and elk populations (Freddy 1982, Rooseberry and Woolf 1991). We used Pearson correlation analysis to estimate the effects of the total daily snow depths for November of each year to examine effects of snow on hunter success.

Nutritional Condition (Predictions 3, 4, and 5)

We collected and analyzed femur marrow from dead radiotagged cervids and from cougar and wolf-killed cervids found by snowtracking and other methods (Kunkel 1997). Samples were double-wrapped in plastic and kept frozen until analysis. We used the dry mass of the marrow (60°C for 48 hr) expressed as a percentage of its fresh mass to estimate percent fat (Neiland 1970).

Following the methods of Gasaway et al. (1992) and Carbyn et al. (1993), we considered predation on deer <10 years old (Nelson and Mech 1990), elk ≤12 years old (Houston 1982), and moose ≤15 years old (Gasaway et al. 1992) additive to other causes of mortality such as malnutrition and senescence. Further, we considered predation to be additive on deer with >25% femur marrow fat (FMF; Cheatum 1949), elk with >35% FMF (Bubenik 1982), and moose with >20% FMF (Peterson et al. 1984).

Factors Explaining Cervid Population Trends (Prediction 4)

We assessed the relative contributions of snow depth, (number of days with >30 cm snow on the ground; Fuller 1991, Pauley et al. 1993), animal condition (% FMF of deer killed by cougars and wolves), diastema lengths of yearling male deer, and minimum number of wolves present in May (Pletscher et al. 1997) to elk and deer population trends as estimated by hunter success by computing Pearson correlations and partial correlations with stepwise multiple-regression analysis. We thereby tested for the effect of limiting factors while controlling for the effect of other potentially confounding factors. This procedure is similar to key-factor analysis (Varley and Gradwell 1960, Messier 1991).

We used Pearson correlations to associate annual deer survival rates, annual elk survival rates, and annual moose survival rates to each other and to the number of days with >30 cm of snow on the ground.

RESULTS

Survival Rates

We radiotagged 67 female deer, 55 female elk, and 49 female moose. Median capture age was 4.5 years (5 fawns, 8 yearlings, 44 ≥2 yr old) for deer, 6.5 years (6 calves, 7 yearlings, 42 ≥2 yr old) for elk, and 6.5 years (4 yearlings, 42 ≥2 yr old) for moose.

Daily survival rates for deer during August and September were higher than all other months ($P < 0.05$); therefore, 3 intervals were defined where survival was constant: (1) June–July, (2) August–September, and (3) October–May. Forty-two (66%) deer died during the study period, which resulted in an overall annual survival rate of 0.74 (Table 1). The annual deer survival rate in 1991 (0.62) was lower than the annual survival rate in 1992 ($Z = 1.98$, $P = 0.05$).

Table 1. Age-specific survival rates of female white-tailed deer in and near Glacier National Park, Montana, from January 1990 through June 1996.

	June–July			August–September			October–May			Annual[b]	
Class	n[a]	Rate	95% CI	n	Rate	95% CI	n	Rate	95% CI	Rate	95% CI
≤2 yr	636	1.00	1.00–1.00	600	1.00	1.00–1.00	5,534	0.77	0.62–0.95	0.77	0.62–0.95
3–6 yr	3,414	0.98	0.95–1.00	3,337	0.98	0.95–1.00	13,656	0.73	0.63–0.84	0.70	0.60–0.83
≥7 yr	3,276	0.89	0.82–0.98	3,063	1.00	1.00–1.00	9,364	0.81	0.70–0.94	0.73	0.61–0.86
All	8,302	0.94	0.91–0.98	7,950	0.98	0.96–1.00	33,061	0.80	0.74–0.86	0.74	0.68–0.80

[a] n = 49,353.
[b] Radio days.

For female elk, 4 intervals were defined where survival was constant: (1) June–September, (2) October–November, (3) December–February, and (4) March–May. Twenty-eight (53%) elk died during the study period, which resulted in an overall annual survival rate of 0.83 (Table 2). The annual elk survival rate in 1991 (0.64) was lower than the annual survival rate in 1992 (0.88; $Z = 2.02$, $P = 0.04$).

For female moose, 4 intervals were defined where survival was constant: (1) June–July, (2) August–October, (3) November–February, and (4) March–May. Twenty-one (47%) moose died during the study period, which resulted in an overall annual survival rate of 0.88 (Table 3). Survival rates of moose did not differ among years ($P > 0.05$).

Recruitment and Rate of Change

Fawn:doe ratios (expressed as fawns:100 does) obtained from roadside counts were similar to ratios obtained from radiotagged does (1994: 25.4 vs. 30.0; 1995: 31.9 vs. 37.0; 1996: 30.4 vs. 33.0). The rate of change (λ) for the deer population was <1.0 for all years (Table 4).

Lambda for elk was <1.0 for all years (Table 5). Lambda for moose was >1.0 before 1994 but was <1.0 for 1995 and 1996 (Table 6).

Pellet and Aerial Counts

The mean number of deer pellet groups per plot declined from 1990 (0.46, $n = 480$ plots; Table 4) to 1992 (0.29; $P < 0.05$), from 1992 to 1994 (0.16; $P = 0.01$), and from 1994 to 1996 (0.11; $P < 0.05$). The trend was similar when we compared 960 plots annually.

The mean number of elk pellet groups per plot increased from 1991 (0.08, $n = 960$ plots; Table 5) to 1993 (0.18; $P < 0.05$) and declined from 1993 to 1996 (0.11; $P < 0.05$). Based on helicopter surveys, the estimated number of elk in the core study area was lower in 1994 (287) than 1993 (619; $P < 0.001$; Table 5).

Hunter Success

The number of hunter-days per deer harvested increased from 1990 to 1996 ($r = 0.73$, $P = 0.01$; Table 4). The number of hunter-days per elk harvested increased from 1991 to 1996 ($r = 0.69$, $P = 0.01$; Table 5).

Cause-Specific Mortality Rates (Prediction 1)

Cougars were the most common cause of mortality for deer, accounting for 14 deaths (33%; Table 7). Wolf predation resulted in 10 deaths. Cougars were also the most common cause of mortality for elk, accounting for 12 deaths (43%; Table 8). Bears were the most common causes of mortality for moose, accounting for 7 deaths (33%; Table 9).

Effect of Age on Survival (Prediction 2)

The annual survival rate was lower for 4–5-year-old deer (0.57) than the annual survival rate for 2–3-year-old deer (0.85; $Z = 2.57$, $P = 0.01$). Survival rates were similar when ages were grouped into 3 classes (≤2, 3–6, ≥7 yr; $P > 0.10$, $\beta = 0.85$; Table 1).

The annual survival rate of elk ≤2 years old (0.59) was lower than the annual survival rate for elk 3–7 years old (0.93; $Z = 2.50$, $P = 0.01$; Table 2). The annual survival rate for elk 3–7 years old was greater than the rate for elk ≥8 years old (0.79; $Z = 2.50$, $P = 0.01$).

The cougar-caused mortality rate on elk ≤2 years old (0.23) was greater than the cougar-caused mortality rate on 3–7-year-old elk (0.01; $Z = 2.09$, $P = 0.04$). The cougar-caused mortality rate on elk ≥8 years old (0.07) was greater than the rate on 3–7-year-old elk ($Z = 2.00$, $P = 0.05$). Wolf-caused mortality rates were not different among ≤2-year-old elk (0.07), 3–7-

Table 2. Age-specific and annual survival rates of female elk in and near Glacier National Park, Montana, from January 1990 through June 1998.

Class	June–September			October–November			December–February			March–May			Annual[a]		
	n[b]	Rate	95% CI	n	Rate	95% CI	n	Rate	95% CI	n	Rate	95% CI	Rate	95% CI
≥2 yr	1,316	1.00	1.00–1.00	576	0.90	0.73–1.00	1,004	0.76	0.56–1.00	1,276	0.87	0.71–1.00	0.59	0.39–0.90
3–7 yr	6,222	1.00	1.00–1.00	3,001	0.94	0.88–1.00	5,485	1.00	1.00–1.00	6,062	0.98	0.96–1.00	0.93	0.86–1.00
≥8 yr	9,368	0.97	0.94–1.00	4,401	0.91	0.84–0.98	7,416	0.97	0.94–1.00	7,891	0.91	0.85–0.97	0.79	0.71–0.88
All	16,908	0.99	0.97–1.00	7,978	0.92	0.87–0.97	13,634	0.97	0.94–1.00	14,058	0.94	0.91–0.98	0.83	0.77–0.89

[a] n = 58,578.
[b] Radio days.

year-old elk (0.02) or ≥8-year-old elk (0.02; $Z = 0.71$, $P > 0.10$). The grizzly-caused mortality rate was marginally greater on ≥8-year-old elk (0.04) than on 3–7-year-old elk (0.00; $Z = 1.71$, $P = 0.09$).

Moose 11–17 years old had a lower survival rate (0.80) than moose 3–10 years old (0.93; $Z = 2.17$, $P = 0.03$; Table 3).

Additive Versus Compensatory Mortality (Prediction 3)

Thirty-four of 38 (89%) radiotagged deer killed by predators were ≤10 years old. The mean FMF of deer killed by predators was 67% (range = 6–95%); only 1 deer killed by predators had a FMF <25%. Twenty of 29 (69%) radiotagged elk killed by predators were ≤12 years old. The mean FMF of predator-killed elk was 60% (range = 17–92%); only 1 elk killed by predators had FMF level <35%. Sixteen of 21 moose cows (76%) killed by predators in our study were ≤15 years old. The mean FMF of moose killed by predators was 74% (range = 41–89%).

Ninety-two percent of all nonradiotagged deer and 94% of all nonradiotagged moose killed by wolves and cougars since 1986 had FMF values >20% (deer: $\bar{x} = 71\%$, $n = 244$; moose: $\bar{x} = 65\%$, $n = 32$). Ninety-five percent of elk killed during the same period had FMF values >35% ($\bar{x} = 71$, $n = 76$).

Among nonradiotagged cervids killed by wolves and cougars since 1986, 93% of all deer were younger than 10 years old, 90% of all elk were <12 years old, and 90% of all moose were younger than 15 years old.

Predators (including humans) were responsible for >90% of all cervid mortality. As such, it followed that whenever the predation rate of a particular predator on a particular cervid increased in a given year, survival rates of that cervid declined by that same margin, thus providing evidence for the additive effects of predation (Tables 4–9). This additive effect is illustrated by lack of correlation in the predation rates of the 2 most significant predators on deer, wolves and cougars ($r = 0.03$, $P = 0.96$). When cougar predation rates increased, annual deer survival rates decreased.

Factors Explaining Declines (Prediction 4)

Deer.—Annual survival rates were negatively correlated with the number of days per winter with >30 cm of snow on the ground ($r = 0.72$,

Table 3. Age-specific and annual survival rates of female moose in and near Glacier National Park, Montana, from January 1990 through June 1996.

Class	June–July			August–October			November–February			March–May			Annual[a]		
	n[b]	Rate	95% CI	n	Rate	95% CI	n	Rate	95% CI	n[b]	Rate	95% CI	Rate	95% CI
≤3 yr	336	0.77	0.46–1.00	276	1.00	1.00–1.00	811	1.00	1.00–1.00	920	1.00	1.00–1.00	0.77	0.46–1.00
3–10 yr	6,305	0.98	0.95–1.00	9,371	1.00	1.00–1.00	14,035	0.98	0.96–1.00	11,823	0.96	0.93–1.00	0.93	0.88–0.97
≥11 yr	3,055	0.82	0.65–1.00	4,421	0.98	0.94–1.00	5,866	0.92	0.85–1.00	4,386	0.96	0.90–1.00	0.80	0.70–0.91
All	9,596	0.96	0.92–0.99	14,068	0.99	0.98–1.00	19,574	0.97	0.94–0.99	15,166	0.96	0.94–0.99	0.88	0.84–0.93

[a] n = 40,404.
[b] Radio days.

P = 0.06; Table 4). Hunter-days per deer harvested (deer population trend) was not correlated with total snow depth during the November hunting season ($r = -0.07$, $P = 0.85$) or number of days per winter (previous) with >30 cm snow ($r = -0.30$, $P = 0.38$). Hunter-days per deer harvested was correlated with hunter-days per elk harvested ($r = 0.79$, $P = 0.004$) and marginally with wolf numbers ($r = 0.53$, $P = 0.09$). Hunter-days per deer harvested was not correlated with the mean FMF of deer killed by wolves and cougars ($r = -0.12$, $P = 0.80$), nor with mean diastema length of yearling male deer killed by hunters ($r = 0.26$, $P = 0.43$). Wolf numbers explained more of the increase in hunter-days per deer (deer decline) than did snow depth or diastema length ($r = 0.53$, $P = 0.09$).

Elk.—Annual survival rates of elk were not correlated with the number of days per winter with >30 cm of snow on the ground ($r = 0.41$, $P = 0.42$). Annual elk survival rates were marginally correlated with annual deer survival rates ($r = 0.78$, $P = 0.07$).

We found no relation between hunter-days per elk harvested (elk population trend) and depth of snow in November ($r = -0.36$, $P = 0.92$) or number of days per winter (previous) with >30 cm snow ($r = 0.05$, $P = 0.89$, $n = 11$). Hunter-days per elk harvested was correlated with wolf numbers ($r = 0.58$, $P = 0.06$). Wolf numbers explained more of the increase in hunter-days per elk (elk decline) than did snow depth ($r = 0.58$, $P = 0.08$).

Moose.—Annual survival rates of moose were not correlated with the number of days per winter with >30 cm of snow on the ground ($r = 0.32$, $P = 0.55$).

Effect of Wolf and Alternative Prey Densities on Survival (Prediction 5)

The November–February interval survival rate of moose living in wolf territories (0.90, $n = 35$) was lower than the interval survival rate for moose outside wolf territories (1.00; $Z = 2.58$, $P = 0.01$, $n = 13$). The annual survival rate for moose living in wolf territories (0.82, $n = 25$) was not different than the rate of moose outside wolf territories (0.90; $Z = 1.35$, $P = 0.18$, $n = 13$).

The wolf-caused mortality rate for moose in areas without wintering deer (0.08, $n = 13$) was greater than that for moose in areas with wintering deer (0.00; $Z = 2.09$, $P = 0.04$, $n = 4$).

Table 4. Population trend indices for white-tailed deer in and near Glacier National Park, Montana, 1986–98.

Year	Hunter-days/deer	Pellets/plot		S[a]		Fawns/doe		Lambda		No. days >30 cm snow
		n	SE	Rate	95% CI	n	SE	λ	95% CI	
1986	12.6									57
1987	19.9									76
1988	37.8									7
1989	32.7									85
1990	27.7	0.46	0.04			0.39	0.05			69
1991	19.7	0.32	0.04	0.62	0.47–0.82	0.34	0.03	0.75	0.53–0.39	104
1992	34.4	0.29	0.04	0.84	0.71–1.00	0.33	0.02	0.98	0.81–1.18	13
1993	38.6	0.37	0.05	0.76	0.62–0.93	0.35	0.03	0.94	0.68–1.07	105
1994	38.5	0.16	0.02	0.71	0.57–0.90	0.35	0.03	0.90	0.62–1.04	70
1995	24.9	0.16	0.02	0.72	0.57–0.90	0.32	0.02	0.92	0.65–1.06	74
1996	35.8	0.11	0.02	0.80	0.64–0.80	0.30	0.03	0.92	0.72–1.18	30

[a] Survival rate for radiotagged female deer.

North Fork Versus Regional Trends (Prediction 5)

Deer.—In contrast to our study area, hunter-days per deer harvested in northwest Montana were negatively correlated with year, declining from 1987 to 1995 ($r = -0.71$, $P = 0.03$). The mean (± SE) diastema length of yearling males brought through the North Fork check station from 1992 to 1996 (70.7 ± 0.9, $n = 33$) was higher than the mean from 2 other check stations in northwestern Montana (Olney: 67.9 ± 0.3 mm, $n = 272$, Duncan's multiple-range test $P < 0.05$; Swan Valley: 68.0 ± 0.3 mm, $n = 376$, Duncan's multiple-range test $P < 0.05$). The mean diastema length of yearling males for all check stations in northwestern Montana combined declined from 1985 to 1995 ($r = -0.78$, $P = 0.008$), while there was no change in the North Fork ($r = 0.13$, $P = 0.14$).

Elk.—Unlike the North Fork, hunter-days per elk harvested in northwestern Montana did not change significantly from 1987 to 1995 ($r = 0.16$, $P = 0.67$). The sample size of diastema from yearling male elk from the North Fork check station was too small to compare with other check stations in northwestern Montana.

DISCUSSION

All the individual population indices clearly pointed to a significant decline in the deer population, and all but 1 (pellet counts) pointed to a decline for elk. Elk distribution during winter in our study area was more affected by winter severity than was deer distribution (Bureau 1992, Rachael 1992). As a result, distribution of elk pellets probably varied more among winters than distribution of deer pellets, and pellet trend may reflect elk distribution more than elk population.

Additive and compensatory effects fall along

Table 5. Population trend indices for elk in and near Glacier National Park, Montana, 1986–96.

Year	Hunter days/elk	Count[a]		Pellets/plot		S[b]		Calves:cow[c]		Lambda	
				n	SE	Rate	95% CI	n	SE	λ	95% CI
1986	34.9										
1987	38.9										
1988	73.9										
1989	73.5										
1990	151.1										
1991	83.7			0.08	0.01	0.64	0.47–0.88	0.41	0.08	0.77	0.55–1.00[d]
1992	85.8			0.12	0.01	0.88	0.77–1.00	0.16	0.02	0.97	0.82–1.09
1993	228.6	619	122	0.18	0.02	0.89	0.77–1.00	0.12	0.01	0.94	0.81–1.07
1994	113.3	287	34	0.06	0.01	0.82	0.69–0.98	0.14	0.03	0.88	0.73–1.07
1995	107.2	382	106	0.09	0.01	0.89	0.78–1.00	0.16	0.05	0.96	0.82–1.11
1996	260.3	396	183	0.11	0.01	0.84	0.72–0.98	0.13	0.04	0.90	0.75–1.07

[a] Survival rate for radiotagged female elk.
[b] From spring helicopter survey, except 1991 and 1992, which were from airplane; 90% confidence interval.
[c] From spring helicopter survey; 90% confidence interval.
[d] Lambda 95% confidence interval.

Table 6. Population trend indices for moose in and near Glacier National Park, Montana, 1991–96.

Year	S[a]	95% CI	Calves:cow[b]	Lambs:
1991	0.88	0.76–1.00	0.25	0.50
1992	0.97	0.90–1.00	0.32	1.07
1993	0.85	0.73–0.98	0.44	1.04
1994	0.90	0.79–1.00	0.30	1.03
1995	0.84	0.73–0.96	0.10	0.83
1996	0.81	0.68–0.96	0.09	0.85

[a] Survival rate for radiotagged female moose.
[b] Based on calves seen with radiotagged cows during spring, except 1995 and 1996, which was the ratio of all calves and cows seen from the air in November.

a continuum. Predation by multiple predators in the North Fork occurs toward the additive end of the spectrum. Wolf and cougar predation rates on deer were not correlated. Both wolves and cougars readily took prime-aged deer and deer that, based on FMF content, probably would have survived the winter had they not been killed by predators. We do acknowledge that other stressors may result in the death of an animal even if FMF value is high (Mech et al. 1995). However, we found only 8 winter-killed elk and deer in 5 years.

Mortality agents have generally been considered additive when cervid populations are well below carrying capacity (Gasaway et al. 1983, Ballard and Larsen 1987, Gauthier and Theberge 1987, Gasaway et al. 1992). Filonov (1980) found a high degree of substitution among mortality factors acting on moose, red deer (*Cervus elaphus*), sika deer (*Cervus nippon*), roe deer (*Capreolus capreolus*), and reindeer (*Rangifer tarandus*) on reserves in the former Soviet Union. Despite this conclusion, she reported that mortality of ungulates was highest during years of high wolf density. Additionally,

Table 7. Annual cause-specific mortality rates of female white-tailed deer in and near Glacier National Park, Montana, from January 1990 through June 1996.

Source	n (%)	Rate	95% CI[a]
Wolves	10 (24)	0.06	0.03–0.10
Humans	5 (12)	0.03	0.00–0.06
Bears	4 (10)	0.03	0.00–0.05
Cougars	14 (33)	0.08	0.04–0.13
Coyotes	2 (05)	0.01	0.00–0.03
Wolf–cougar	1 (02)	0.01	0.00–0.01
Unknown predator	2 (05)	0.01	0.00–0.03
Old age[b]	1 (02)	0.01	0.00–0.02
Unknown	3 (07)	0.02	0.00–0.04

[a] 99,333 radio days.
[b] Complications from pneumonia.

Table 8. Cause-specific mortality rates of female elk in and near Glacier National Park, Montana, from January 1990 through June 1996.

Source	n (%)	Rate	95% CI[a]
Cougar	12 (43)	0.06	0.02–0.10
Human	6 (21)	0.04	0.01–0.08
Wolf	3 (11)	0.03	0.00–0.05
Grizzly	3 (11)	0.03	0.00–0.04
Bear–wolf	3 (11)	0.03	0.00–0.04
Unknown	1 (04)	0.01	0.00–0.02

[a] 33,578 radio days.

much of the compensatory response she observed occurred when prey was probably at or above carrying capacity. Human-caused mortality (hunting) was additive to other mortality of adult female white-tailed deer in 3 areas of Montana (Dusek et al. 1992).

Little is known about how alternative prey affect cervid–wolf systems (Messier 1994). Alternative prey may either dilute or exacerbate the effects of the predator on the primary prey. Dilution (by diversion) might be expected where alternative prey is more vulnerable (Pimlott et al. 1969, Carbyn 1983, Potvin et al. 1988), whereas exacerbation might be expected where the alternate prey produces a numerical response in the predator. Exacerbation or dilution effects are probably not mutually exclusive and may best be described as a continuum that occurs over time. Fuller (1990) believed the effect of wolves on deer in northeastern Minnesota was exacerbated by the abundance of moose. Tests of the dilution or exacerbation theories have not been conducted. The dilution theory seems most plausible within our study area, at least over the short term, where deer and moose coexist. Where deer were present in our study area, the wolf-caused mortality rate

Table 9. Cause-specific mortality rates of female moose in and near Glacier National Park area, Montana, from January 1990 through June 1996.

Source	n (%)	Rate	95% CI[a]
Grizzly	5 (24)	0.03	0.00–0.05
Wolf	5 (24)	0.03	0.00–0.05
Human	3 (14)	0.02	0.00–0.04
Bear	2 (10)	0.01	0.00–0.03
Unknown	2 (10)	0.01	0.00–0.03
Bear–wolf	1 (05)	0.01	0.00–0.02
Accident	1 (05)	0.01	0.00–0.02
Unknown predator	1 (05)	0.01	0.00–0.02
Injury–pneumonia	1 (05)	0.01	0.00–0.02

[a] 49,404 radio days.

on moose was significantly lower than in areas where deer were absent.

The presence of deer on moose summer ranges may have diverted wolf predation from moose and allowed moose numbers to increase despite the presence of 3 species of predators. Densities of moose in our study area (0.42–0.55/km^2; Langley 1993) are higher than the mean density of moose in areas in Alaska and Yukon where wolves and bears are only lightly harvested (0.15/km^2; Gasaway et al. 1992), but they are not as high as densities in other systems where ungulates assumed to be more vulnerable than moose are also found (0.6–1.3 km^2; Bergerud 1992). The moose density in our study area is at the upper end of the range that Messier (1994) referred to as low-density equilibrium where predation may regulate numbers.

We could not compare mortality rates of deer or elk in the presence and absence of each other, because spatial separation did not occur. However, we did find a correlation between the decline of elk, the preferred prey for wolves in our study area (Kunkel 1997), and an increase in selection of deer by wolves (Kunkel 1997). This change in selection may exacerbate, in the long term, the decline in elk numbers because the presence of deer may maintain wolf numbers and predation pressure on elk. Deer have a higher reproductive potential than elk and can likely withstand greater predation pressure than elk. Where deer occur at high densities relative to elk, and both wolves and cougars are present, we hypothesize cycling in deer populations and low density equilibriums in elk.

With the addition of a new population of predator (wolves) to an existing multipredator system, our results indicated that deer and elk populations declined and, based on our 5 predictions, that predation was the primary factor limiting these populations. The overall trend in the moose population was not as clear, but based on agreement with 4 of the 5 predictions, predation was the primary factor affecting the population. If deer had been less available in this system, the effect of predation on moose likely would have been greater.

MANAGEMENT IMPLICATIONS

As wolves continue to recolonize the western United States, managers must be especially alert to changes in cervid populations and their causes, especially in those areas where multiple predators are present. Managers should expect lower cervid populations that may remain low for extended periods where wolves, bears, cougars, and humans vie for the same prey (Gasaway et al. 1992, National Research Council 1997). Lower cervid densities may in turn ultimately yield lower predator densities and thus slow wolf and grizzly recovery (McLellan and Hovey 1995, Boertje et al. 1996).

Near the end of our study, we began to see what may become a significant decline in wolf and cougar density that may allow some prey recovery (Kunkel 1997; T. K. Ruth, Hornocker Wildlife Institute, unpublished data). Depending on management objectives, managers should be prepared to reduce hunting pressure on cervids to prevent potentially long-term low equilibriums for prey where multiple predators are limiting prey populations (Gasaway et al. 1983, Fuller 1990, Boertje et al. 1996). Habitat improvement and manipulation of alternative prey may also benefit prey populations (Boertje et al. 1995, Kunkel 1997). Enhancement of deer populations may divert predation pressure on moose, and reduction of deer populations may reduce wolf density and predation levels on elk, although more research is necessary to substantiate these hypotheses.

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LITERATURE CITED

BALLARD, W. B., AND D. C. LARSEN. 1987. Implications of predator–prey relationships to moose management. Swedish Wildlife Research 1 (Supplement):581–602.

BERGERUD, A. T. 1992. Rareness as an antipredator strategy to reduce predation risk for moose and caribou. Pages 1008–1021 in D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, London, United Kingdom.

BOERTJE, E. D., D. C. KELLYHOUSE, AND R. D. HAYES. 1995. Methods for reducing natural predation on moose in Alaska and Yukon: an evaluation. Pages 505–513 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute Occasional Publication 35.

———, P. VALKENBURG, AND M. E. MCNAY. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60:474–489.

BOYD, D. K., E. E. REAM, D. H. PLETSCHER, AND M. W. FAIRCHILD. 1994. Prey taken by colonizing wolves and hunters in the Glacier National Park area. Journal of Wildlife Management 58:289–295.

BUBENIK, A. B. 1982. Physiology. Pages 125–179 in J. W. Thomas and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

BURKEAD, M. J. 1992. Mortality and seasonal distribution of elk in an area recently colonized by wolves. Thesis, University of Montana, Missoula, Montana, USA.

CARBYN, L. N. 1983. Wolf predation on elk in Riding Mountain National Park. Journal of Wildlife Management 47:963–976.

———, S. M. OOSENBRUG, AND D. W. ANIONS. 1993. Wolves, bison, and the dynamics related to the Peace–Athabasca Delta in Canada's Wood Buffalo National Park. Canadian Circumpolar Institute Research Series Report 4.

CHEATUM, E. L. 1949. Bone marrow as an index to malnutrition in deer. New York State Conservationist 3:19–22.

CLOWER, M. R. 1956. Single-gate deer trap. California Fish and Game 42:199–201.

DUSEK, G. L., A. K. WOOD, AND S. T. STEWART. 1992. Spatial and temporal patterns of mortality among female white-tailed deer. Journal of Wildlife Management 56:645–650.

FULLAGAR, C. 1980. Predator–prey problems in nature reserves of the European part of the RSFR. Journal of Wildlife Management 44:399–396.

FREDDY, D. J. 1982. Predicting mule deer harvest in Middle Park, Colorado. Journal of Wildlife Management 46:801–806.

FRISINA, M. R., AND K. S. DOUGLASS. 1989. Using diastema length as an indicator of body condition in fawn and yearling mule deer. Proceedings of the Montana Academy of Science 49:23–26.

FULLER, T. K. 1990. Dynamics of a declining white-tailed deer population in north-central Minnesota. Wildlife Monographs 110.

———. 1991. Effect of snow depth on wolf activity in northcentral Minnesota. Canadian Journal of Zoology 69:283–287.

GASAWAY, W. D., R. D. BOERTJE, D. V. GRANGAARD, D. G. KELLEYHOUSE, R. O. STEPHENSON, AND D. G. LARSON. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120.

———, R. O. STEPHENSON, J. L. DAVIS, P. E. K. SHEPHERD, AND O. E. BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84.

GAUTHIER, D. A., AND J. B. THEBERGE. 1987. Wolf predation. Pages 119–127 in M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Trappers Association, Toronto, Ontario, Canada.

GILBERT, F. F. 1966. Aging white-tailed deer by annuli in the cementum of the first incisor. Journal of Wildlife Management 30:200–202.

HARTTGOEN, A. M. 1977. Problems relating to capture. Animal Regulation Studies 1:23–46.

HAUTER, I. W., AND W. A. BERGERUD. 1991. Moose recruitment, adult mortality, and rate of change. Alces 27:65–73.

HEISEY, D. M. 1995. Micromort user's guide. NH Analytical Software, St. Paul, Minnesota, USA.

———, AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49: 668–674.

HOUSTON, D. B. 1982. The Northern Yellowstone elk: ecology and management. Macmillan, New York, New York, USA.

HUDSON, D. J. 1983. Prey selectivity of wolves in Banff National Park. I. Prey species. Canadian Journal of Zoology 71:130–139.

JENKINS, K. J. 1985. Winter habitat and niche relationships of sympatric cervids along the North Fork of the Flathead River, Montana. Dissertation, University of Idaho, Moscow, Idaho, USA.

KRAHMER, R. W. 1989. Seasonal habitat relationships of white-tailed deer in northwestern Montana. Thesis, University of Montana, Missoula, Montana, USA.

KUNKEL, K. E. 1997. Predation by wolves and other large carnivores in northwestern Montana and southeastern British Columbia. Dissertation, University of Montana, Missoula, Montana, USA.

LANGLEY, M. A. 1993. Habitat selection, mortality, and population monitoring of whitas moose in the North Fork of the Flathead Valley, Montana. Thesis, University of Montana, Missoula, USA.

LEOPOLD, A. 1933. Game management. Charles Scribner's Sons, New York, New York, USA.

MCLELLAN, B. N. 1989. Population dynamics of grizzly bears during a period of resource extraction development. I. Density and age–sex composition. Canadian Journal of Zoology 67:1856–1860.

———, AND F. W. HOVEY. 1995. The diet of grizzly bears in the Flathead River drainage in southeastern British Columbia. Canadian Journal of Zoology 73:704–712.

MECH, L. D., T. J. MEIER, J. W. BURCH, AND L. G.

ADAMS. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. Pages 331–343 in L. N. Carbyn, S. H. Fritts, and D. E. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute Occasional Publication 35.

MESSIER, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. Journal of Animal Ecology 60:377–393.

———. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478–488.

MIDDLEMAN, T., J. D. PORT, T. H. STANLEY, AND D. F. WILLARD. 1984. Immobilization of elk and moose with carfentanil. Journal of Wildlife Management 48:258–261.

NATIONAL RESEARCH COUNCIL. 1997. Wolves, bears, and their prey in Alaska: biological and social challenges of wildlife management. National Academy Press, Washington, D.C., USA.

NEILAND, K. A. 1970. Weight of dried marrow fat in caribou femurs. Journal of Wildlife Management 34:904–907.

NELSON, M. E., AND L. D. MECH. 1990. Weights, productivity, and mortality of old white-tailed deer. Journal of Mammalogy 71:689–691.

O'GARA, B. W. 1978. Differential characteristics of predator kills. Proceedings of the Biennial Pronghorn Antelope Workshop 8:380–393.

PAULEY, G. R., J. M. PEEK, AND P. ZAGER. 1993. Predicting white-tailed deer habitat use in northern Idaho. Journal of Wildlife Management 57:304–313.

PETERSON, R. O., J. D. WOOLINGTON, AND T. N. BAILEY. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88.

PIMLOTT, D. H., J. A. SHANNON, AND G. B. KOLENOSKY. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Department of Lands and Forest Restoration Report 87.

PLETSCHER, D. H., R. R. REAM, D. K. BOYD, M. W. FAIRCHILD, AND K. E. KUNKEL. 1997. Dynamics of a recolonizing wolf population. Journal of Wildlife Management 61:459–465.

POTVIN, F., H. JOLICOEUR, L. BRETON, AND R. LEMIEUX. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. Canadian Journal of Zoology 66:1274–1279.

RACHEAL, J. S. 1982. Mortality and seasonal distribution of white-tailed deer in an area recently recolonized by wolves. Thesis, University of Montana, Missoula, Montana, USA.

REAM, R. R., M. W. FAIRCHILD, D. K. BOYD, AND A. BLAKESLEY. 1989. First wolf den in western U.S. in recent history. Northwestern Naturalist 70:39–40.

REIMERS, E. 1972. Growth in domestic and wild reindeer in Norway. Journal of Wildlife Management 36:613–619.

ROCE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–235.

ROOSEBEEK, J. I., AND A. WOOLF. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife Monographs 117.

SINGER, F. J. 1979. Habitat partitioning and wildfire relationships of cervids in Glacier National Park, Montana. Journal of Wildlife Management 43: 437–444.

U.S. FISH AND WILDLIFE SERVICE. 1987. Northern Rocky Mountain Wolf Recovery Plan. U.S. Fish and Wildlife Service, Denver, Colorado, USA.

———. 1994. The reintroduction of gray wolves to Yellowstone National Park and central Idaho. Final Environmental Impact Statement. U.S. Fish and Wildlife Service, Denver, Colorado, USA.

———. 1996. Montana wolf recovery report. U.S. Fish and Wildlife Service, Helena, Montana, USA.

VAN BALLENBERGHE, V., AND W. B. BALLARD. 1984. Limitation and regulation of moose populations: the role of predation. Canadian Journal of Zoology 72:2071–2077.

VARLEY, G. C., AND G. R. GRADWELL. 1960. Key factors in population studies. Journal of Animal Ecology 29:399–401.

WEAVER, J. L. 1994. Ecology of wolf predation amidst high ungulate diversity in Jasper National Park, Alberta. Dissertation, University of Montana, Missoula, Montana, USA.

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