

BEAR PREDATION ON MOOSE: A REVIEW OF RECENT NORTH AMERICAN STUDIES AND THEIR MANAGEMENT IMPLICATIONS

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ABSTRACT: Predation of moose (*Alces alces*) calves by brown bears (*Ursus arctos*), black bears (*Ursus americanus*), and wolves (*Canis lupus*) singly or in combination can significantly limit annual recruitment. Brown bears are often the greatest source of mortality to calves where bear densities exceed 16/1,000 km², even though black bears may be 2-3 times more abundant. Black bears are the largest source of moose calf mortality when they are 10 times more numerous than brown bears and their densities are >200/1,000 km². Minimum average predation by brown bears on neonatal moose ranges from 1 calf/7-12 bear-days in late spring and early summer. Minimum predation rates by black bears on neonatal moose ranged from 1 calf moose/11-53 bear-days. Predation rates on moose calves by grizzly bears appear to be independent of moose density while black bear predation rates may be related to moose densities and occurrence of brown bears. Brown bears can be significant predators of adult moose averaging 1 kill/26-102 bear-days. Black bears are not significant predators of adult moose. During 1 study when brown bear populations were temporarily reduced by ≥60% calf and adult moose survival increased in the short term. Effects on moose populations of lesser bear reductions are unclear and warrant further study. If predator populations must be reduced to favor ungulate populations managers should first reduce wolf or black bear populations that have higher reproductive rates, wider geographic distributions, and are easier to manage than grizzly bear populations.

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Studies concerning relationships between predators and moose were reviewed and updated at the First and Second International Moose (*Alces alces*) Symposiums held at Quebec City, Quebec, Canada in 1973 and Uppsala, Sweden in 1984, respectively. At the First Symposium, wolves (*Canis lupus*) were the only recognized significant predator of moose and Wolfe (1974) concluded that they could exert a regulatory effect if predation focused on calves. At the Second Symposium, reviews by Ballard and Larsen (1987) and Van Ballenberghe (1987) concluded that predation by brown bears (*Ursus arctos*), black bears (*Ursus americanus*), and wolves could singly and in combination constitute a significant source of mortality that could limit and may regulate moose populations. All authors recommended continued long-term studies of the relationships and dynamics of large predators and their ungulate prey, particularly bear-moose relationships.

Since the Second Moose Symposium,

several studies concerning bear-moose relationships have been published or are in press. I summarize results of recent studies concerning bear-moose relationships and address 6 questions:

1. Under what conditions does bear predation become a significant source of mortality to moose populations?
2. Is bear predation an additive or compensatory form of mortality? Under what conditions can it change from one form to another?
3. Are moose survival rates or causes of mortality related to bear and/or moose densities?
4. Are bear predation rates related to densities of bear and/or moose?
5. Can bear predation limit or regulate moose populations? Can brown bears, black bears, or wolves singly regulate or limit moose populations or is a combination of predator species necessary?
6. Once bear predation has been identified as

a significant limiting factor, what options do wildlife managers have?

Definitions

The role of predation in regulating or limiting moose populations is complicated and frequently degenerates into semantic arguments. To avoid confusion, I define terms used in this review.

Limiting factors: responsible for inducing year-to-year changes in the rates of population growth or increase (Messier 1991a, b). Such factors can be composed of density dependent and independent processes.

Regulating factors: a subset of limiting factors; any density-dependent process that keeps an animal population within normal density ranges (Messier 1991a, b).

Predation or kill rate: the number of days/adult or calf moose mortality/individual adult (>2 years age) bear (Ballard *et al.* 1987).

Mortality rate: the percent of calves dying from a particular cause.

Additive mortality: mortality that is noncompensatory and additional to other sources or causes of mortality.

Compensatory mortality: a form of mortality that replaces other forms of mortality. The magnitude of this mortality usually increases with population density.

I classify recent bear studies into 3 related but distinct categories: predation rates, calf moose mortality studies, and bear removal programs. The terms "grizzly bear" and "brown bear" are synonymous.

BEAR PREDATION RATES

Eastcentral Alaska

Boertje *et al.* (1988) studied predation rates of grizzly bears on moose and caribou during autumn 1985 and spring and summer 1986 by daily observing 24 radio-collared bears. Grizzly bear density was estimated at 16/1,000 km². Black bears were thought to be scarce. Moose density was relatively low (175/1,000 km²).

Fifteen adult radio-collared grizzly bears killed a minimum of 45 calves: 31 during spring and 14 during summer. Spring predation rates average 1 calf/7 bear-days while summer rates averaged 1/23 bear-days. No calves were killed during autumn. Predation rates on calves by all sex and age classes of bears combined were greater ($P < 0.05$) during spring than summer. Most adult bears killed calves, but 4 of 9 bears killed 72% of the calves.

Kill rates of calves were minimums as bears consumed calves between flights (Boertje *et al.* 1988). Two of 9 calves were killed and consumed between flights in the spring, whereas calves killed during summer were attended by bears in 10 of 12 instances when flights were made twice daily. These authors suspected that, because calves were larger in summer than spring, it took bears longer to consume them.

Radio-collared grizzly bears were also observed consuming 12 adult moose and 3 adult caribou carcasses. To distinguish between predation and scavenging, all moose and caribou carcasses attributed to predation were necropsied within 36 hours of being sighted; all had been killed by bears. Male grizzlies killed adult moose at a rate of 1/26 bear-days in spring, 1/132 bear-days in summer, and 1/43 bear-days in autumn. Predation rates among seasons were not significantly different ($P > 0.05$). There were no observations of predation on adult moose by male grizzly bears during 30 April through 18 May, while they killed an average of 1 adult moose/17 bear-days during the period 19 May through 10 June. All 6 adult moose killed during the latter period were cows, suggesting increased vulnerability during and following parturition. Each adult male bear was estimated to kill from 3.3-3.9 adult moose/year.

Predation rates of single adult female bears were not significantly different ($P > 0.05$) among seasons. During spring, 6 adult female bears killed 2 adult moose (1/102 bear-days),

4 did not kill adult moose during summer, and 10 bears killed 1 adult moose (1/237 bear-days) and 2 adult caribou (1/118 bear-days). Expanded to an annual basis, each adult female bear without young killed an average 0.6-0.8 adult moose and 0.8-1.2 adult caribou. Females with cubs-of-the-year (COY) did not kill adult moose or caribou during 51 spring and 66 summer bear-days, respectively.

Adult males >8 years of age killed more adult moose than adult females >4 years of age on an annual basis. A greater proportion of male (4 of 5 bears observed >49 days) than female bears were observed consuming adult moose carcasses.

Grizzly bears killed 4 times more ungulate biomass than they scavenged. Biomass available from predation versus scavenging was 11.3, 5.9, and 5.2 kg/bear-day versus 0.5, 0.8, and 4.2 kg/bear-day during spring, summer, and autumn, respectively.

Boertje *et al.* (1988) suggested that grizzly bears may have greater impacts on low versus high density moose populations. Boertje *et al.* (1988) and Ballard *et al.* (1990) compared predation rates between their studies and concluded that grizzly bear predation rates were independent of moose density. Total minimum predation on moose calves was 19-76% greater in the eastcentral Alaska study area than in southcentral Alaska (Ballard *et al.* 1990) for a comparable 20-day calving and post-calving period. Boertje *et al.* (1988) also speculated that grizzly bears may compensate for lower densities of moose calves in eastcentral Alaska by spending more time searching for calves.

Southcentral Alaska

Ballard *et al.* (1981) originally reported that brown bears killed an average of 1 ungulate (calves and adults)/6.1 observation days. Because bears commonly remain with kills for >1 day, predation rates based on observation days likely overestimate kill rates (Fuller and Keith 1980). Consequently, the

rates reported by Ballard *et al.* (1981) were overestimates. During 1981 and 1984 additional data on bear predation rates were gathered and the 1978 data were reanalyzed (Ballard *et al.* 1990). Study areas examined in 1978 had relatively low wolf densities (average 3.6/1,000 km²), and black bears were absent or scarce. Both the 1981 and 1984 study areas were inhabited by black bears (90/1,000 km²) and wolves (2.8/1,000 km²) (Ballard *et al.* 1990). Grizzly bear densities in 1978 averaged about 24/1,000 km² in 1978 (Miller and Ballard 1982) and about 28/1,000 km² in 1981 and 1984 (Miller *et al.* 1987).

Forty-four adult radio-collared grizzly bears and 17 adult radio-collared black bears were monitored from fixed-wing aircraft either once or twice daily during 1978, 1981, and 1984 during late May and June; several of these bears were also monitored during summer 1984 to estimate summer predation rates (Ballard *et al.* 1990).

The 44 radio-collared bears were observed on 82% of 1,121 relocations. They were observed on 65 moose calf kills during 756 bear-days during spring and early summer for an average minimum kill rate of 1/11.7 bear-days. Grizzly bears were observed with an additional 20 carcasses that could have been moose calves. Therefore, the minimum kill rates could have been as high as 1/9.0 bear-days. They were also observed with 13 adult moose carcasses during 590 bear-days for an average rate of 1 adult moose/43.7 bear-days. There were no significant differences ($P > 0.05$) in predation rates among years, sexes, ages, or family classes of bears. Lack of significant differences were attributed to relatively small sample sizes and large variation in rates among individual bears; i. e. range 0-1 calf moose kill/2.8 bear-days. Females with cubs-of-the-year appeared to have the lowest predation rates.

Predation on calf and adult moose declined to relatively low levels during summer; this pattern was similar to studies in eastcentral

Alaska (Boertje *et al.* 1988). Only 1 adult moose kill was observed for 17 bears but observability of the bears was low (44%).

Grizzly bears remained with calf carcasses for 0.4-38.6 hours. Eighty-eight percent of the calf moose carcasses were occupied <12 hours. Adult moose carcasses were attended an average of 66 hours (range = 8-141 hrs).

Black bears in southcentral Alaska had relatively low rates of predation on calf moose, averaging 1 calf/40 bear-days (range = 0/29-1/5.7 bear-days). Male black bears appeared to prey more often on moose calves than females but differences were not significant ($P > 0.05$). No adult moose were killed by radio-collared black bears. No kills of calf or adult moose were observed during summer.

CALF MORTALITY STUDIES

Eastcentral Alaska

As part of a multi-species predator-prey study, Boertje *et al.* (1985) studied the causes of moose calf mortality in a low density moose population (175/1,000 km²) where wolf densities had been reduced by a predator control program (Gasaway *et al.* 1990). Grizzly bear, black bear, and wolf densities were estimated at 16, 8-11, and 4/1,000 km², respectively.

Boertje *et al.* (1985, 1987) collared 33 neonate calves in 1984 (Table 1). Eighteen percent of the calves survived the first year with predation accounting for 85% of the deaths. Eight-four percent of the mortality occurred within 21 days of birth. Fifty-two percent of the calves were killed by grizzly bears followed by wolves and black bears that killed 15.1 and 3.0%, respectively. Twelve percent of the calves died from miscellaneous causes such as drowning.

Kenai Peninsula, Alaska

Franzmann and Schwartz (1986) compared the causes of moose calf mortality in 2 different stages of forest succession on the Kenai Peninsula, Alaska. They tested the

hypothesis that, because black bear density was related to the food resource, bears should be more abundant in older forests and consequently mortality rates on moose calves from black bear predation should be higher in old-growth forest.

Mortality rates of moose calves due to black bear predation in the younger forest (1969 burn) were the same (35%) as those in the older mature forest (1947 burn - 34%) (Table 1). Consequently they rejected their original hypothesis. They found no differences in mortality rates between sexes or twin versus single calves. They concluded that mortality rates of moose calves from black bear predation were independent of moose calf density.

Schwartz and Franzmann (1989, 1991) estimated that black bear densities in the 2 areas were similar (205 and 258 bears/1,000 km² in the 1947 and 1969 burns, respectively). They estimated that each adult bear killed an average of 1.2 and 6.2 moose calves in the 1947 and 1969 burns, respectively. Densities of moose calves were greater in the 1969 burn than in the 1947 burn. Moose densities were 3,700 and 1,000 moose/1,000 km², respectively. Grizzly bear densities for the entire Kenai Peninsula were estimated at 23-28/1,000 km², but actual grizzly density in the study areas in relation to radio-collared calves may have been as low as 12/1,000 km² (C. C. Schwartz, Alaska Dep. Fish and Game, pers. commun.).

Southcentral Alaska

Ballard *et al.* (1981) were the first to report that grizzly bears could be a significant source of moose mortality in North America. Using mortality sensing radio collars (Ballard *et al.* 1979), they determined that grizzly bears were responsible for 79% of the mortalities during the first 6 months of life. Other moose calf mortality studies have subsequently suggested that the most numerous of the bear species was also the most important source of

mortality (Ballard and Larsen 1987). Ballard *et al.* (1990) tested this hypothesis during 1984 by studying causes of moose calf mortality in an area where black bear, grizzly bear, and wolf populations were sympatric.

Grizzly and black bear densities were estimated based on mark-recapture techniques (Miller *et al.* 1987), and wolf densities were based on known numbers within radio-collared packs (Ballard *et al.* 1987). Grizzly bear density was estimated at 28/1,000 km², while black bear density was estimated at 90/1,000 km². Differences in bear density were actually less than that reported in terms of distribution of radio-collared moose calves, but black bears were at least twice as numerous as grizzly bears (Ballard *et al.* 1990). Wolf density was estimated at 2.8/1,000 km².

Forty-six neonate moose calves were radio-collared in 1984 (Table 1 - Area 4). Only 17% of the calves survived to November with predation accounting for 84% of the mortality. Grizzly bears killed 24 (52%), black bears killed 4 (9%), and wolves killed 3 (7%). This pattern of mortality was similar to that reported in all other moose calf mortality studies. Ballard *et al.* (1990) concluded that the causes of moose calf mortality were not directly proportional to predator or moose densities.

New Brunswick

During 1983-85 11 moose calves were radio-collared to assess causes of mortality (Boer 1988). Eighty-two percent of the calves survived. Black bear predation and miscellaneous factors each accounted for 50% of the mortalities (Table 1). Black bears were the only predator species in the study area and Boer (1988) estimated that the population was moderately dense.

Newfoundland

During 1983-88, 88 moose calves were radio-collared to assess causes of mortality in Newfoundland (W. E. Mercer, Newfoundland Wildlife Division, pers. commun.). Sev-

enty percent of the bonded calves survived to November (Table 1). Black bears killed 30% of the calves. Black bear densities were estimated at about 570/1,000 km² (S. Mahoney, Newfoundland Wildlife Division, pers. commun.). No other predator species of moose existed in the area. Moose densities were estimated at >3,000/1,000 km² (W. E. Mercer, pers. commun.).

Southwest Yukon Territory

Larsen *et al.* (1989a) studied the causes of moose calf mortality in southwest Yukon Territory during 1983 and 1985 using methods described by Ballard *et al.* (1979) and Ballard and Larsen (1987) (Table 1). Grizzly bear density was estimated at 16/1,000 km². Black bear densities were not determined but were thought to be similar to grizzly bear densities. Similar to many other moose calf mortality studies, wolf densities were reduced during the study as part of a wolf removal program. Wolf densities in late winter prior to calf mortality studies in 1983 and 1985 were 5.9 and 2.2 wolves per 1,000 km², respectively.

Ninety-five (81%) of 117 radio-collared calves died over a 1 year period (Table 1). Of the 117 calves, 77 (66%) were killed by predators, of which grizzly bears killed 42%. There were no differences ($P > 0.05$) in causes of death between years or between collared and uncollared calves. Of 77 sites analyzed for predator sign, Larsen *et al.* (1989a) observed the predator at 39% of the sites. In contrast to Ballard *et al.* (1979, 1981) and Boertje *et al.* (1988), all but 1 calf moose killed by grizzly bears had been covered with dirt and vegetation.

Between parturition and 20 June, grizzlies and wolves accounted for 60 and 10% of the mortalities, respectively. After that date wolves caused 54% and grizzlies 27% of the mortalities.

Larsen *et al.* (1989a) observed 12 instances of bears feeding on calves: 2 were

Table 1. Causes of mortality and survival rates of radio collared moose calves to November in relation to observed predation rates and predator densities in North America.

Area	Southcentral Alaska				Kenai Peninsula, AK		Southwest Yukon ^{a/}	Eastcentral Alaska	Saskatchewan	New Brunswick	Newfoundland
	Area 1-3	Area 1	Area 4	Areas Pooled	1947 burn	1969 burn					
Years	1977, 1978	1979	1984	1977-84	1977, 1978	1981, 1982	1983, 1985	1984	1982	1983, 1985	1983-88
No. calves	124	28	46	198	47	74	117	33	12	11	88
Causes mortality (%)											
Grizzly Bear	41.9	42.9	52.2	44.0	6.4	2.7	41.9	51.5			
Black bear			8.7	2.0	34.0	35.1	3.4	3.0	50.0	9.1	30.0
Grizzly & Black						2.7					
Wolf	1.6		6.5	2.5	6.4	1.4	17.9	15.2			
Unknown predation	2.4			1.5	4.3	2.7	2.6				
Miscellaneous	4.8	14.3	13.1	8.1	5.5	6.0	6.0	12.1		9.1	
Unknown causes	3.2		2.2	2.5	1.3	1.4	9.4				
Surviving (%)	46.0	42.9	17.4	39.4	44.6	46.5	18.8	18.2	50.0	81.8	70.0
Density (No./1,000 km ²)											
Grizzly Bear	24	10	28	24-28	12-28	12-28	16	16	0	0	0
Black bear	0	0	90	0-90	205	258	16 ^{b/}	8-11	200-400	mod.?	570
Wolf	1.8-3.6	2.3	2.8	1.8-3.6	11	11	4.1 ^{c/}	4.0	low?	0?	0
Moose	650	700	892	650	1,000	3,700	220	175	450	?	3,000
Predation Rate											
Grizzly bear											
calves/bear/day				0.097			0.085 ^{d/}	0.143			
adults/bear/day				0.023				0.022			
Black bear											
calves/bear/day			0.025		0.019 ^{d/}	0.103 ^{d/}					
Source ^{e/}	1	2	3	3, 4	10, 12	9, 12	11	7, 8, 15	5, 13	8	14

^a Causes of mortality and survival rates are annual estimates.

^b Black bear densities were not estimated but were thought to be similar to grizzly bear densities (D. G. Larsen, pers. commun.).

^c Average late winter density for 1983 and 1985.

^d Assumes all mortalities occurred between birth and mid-July, i.e., 60-day period. Derived by dividing estimated number of calves killed by 60 days.

^e 1 = Ballard et al. 1982; 2 = Ballard and Miller 1990; 3 = Ballard et al. 1990; 4 = Ballard et al. 1991; 5 = Beaulieu 1984; 6 = Boer 1988; 7 = Boertje et al. 1987; 8 = Boertje et al. 1988; 9 = Franzmann and Schwartz 1986; 10 = Franzmann et al. 1980; 11 = Larsen et al. 1989; 12 = Schwartz and Franzmann 1991; 13 = Stewart et al. 1985; 14 = W. E. Mercer, pers. commun.; and 15 = R. D. Boertje, pers. commun.

females with COY (16.7%), 5 were with yearling or larger offspring (41.7%), 3 were single males (25.0%), and 2 were unknown sex, age or family status (16.7%). They estimated that 49 adult (>6 years-of-age) grizzly bears would kill 250 calves annually. This extrapolated to about 5.1 calves/adult bear/year or 1 calf moose/11.8 bear-days within a 60-day period.

Forty-six percent ($n = 44$) of 96 calves died by 20 June, 68% ($n = 65$) by 1 Nov, and 75% for the year. There were no significant differences ($P < 0.05$) in annual survival of calf moose between sexes, ages of cows, collared versus uncollared calves, birthdate, or how many days it survived (Larsen *et al.* (1989a).

Grizzly bears, wolves, and hunting accounted for 50, 26, and 9 % of the annual mortalities ($n = 534$) to the moose population. Mortalities of calves compared to adults and yearlings were 61 versus 16% by grizzlies, 25 versus 30% by wolves, and 0 versus 39% by hunting. Predation by grizzly bears was the dominant proximate cause of all major sources of moose mortality and the major factor limiting moose population growth.

BEAR REMOVAL PROGRAMS

Since the Second Moose Symposium, several studies have attempted to evaluate the role of bear predation in limiting moose populations. These studies have reduced bear densities through sport hunting or experimental removal programs. All black bear removal studies were conducted as agency control programs while grizzly bear programs have attempted to lower grizzly bear densities by liberalizing sport hunting seasons and increasing bag limits.

Eastcentral Alaska

Gasaway *et al.* (1990) evaluated the roles of wolf and grizzly bear predation in eastcentral Alaska by reducing wolf and bear densities through agency control programs and by liberalizing bear hunting seasons and bag limits.

Reduced wolf densities failed to significantly ($P > 0.05$) improve moose calf survival. Moose calf mortality studies (Boertje *et al.* 1987) suggested that wolves were not the predominant limiting factor of moose calf survival. Grizzly bear densities had been estimated at 16/1,000 km². Between 1982-88, annual bear harvest rates averaged 8%. This harvest rate probably exceeds sustained yield levels (Miller 1990) and would cause a slow decline in the bear population but would not likely produce large measurable changes in calf survival. Gasaway *et al.* (1990) reported that recruitment appeared to improve as a result of the predator control programs but the differences were not statistically significant ($P > 0.05$). They concluded that, had the numbers of the predominant predator (i.e., grizzly bears) been severely reduced, moose calf survival would have significantly increased.

Southcentral Alaska

During the 1980's management biologists attempted to reduce grizzly bear densities over large areas of southcentral Alaska through liberalized sport hunting regulations (Miller 1990). These efforts were the result of moose calf mortality studies and significant increases in moose calf survival following a 60% experimental reduction in bear densities (Ballard *et al.* 1981, Ballard and Larsen 1987, Ballard and Miller 1990). Unfortunately, these reduction efforts were not accompanied by specific management objectives or research proposals to evaluate effects on bears or moose (Miller and Ballard 1992). The bear population was reduced by about 36% between 1980 and 1987. The moose population in southcentral Alaska increased during this period (Ballard *et al.* 1991), but isolating factors responsible for the increase were impossible. Ballard *et al.* (1991:67) stated "lower predator densities, mild winters, and conservative harvest strategies resulted in an increase in the moose population". Reductions in bear density may have altered the rate of

increase in the moose population, but it probably would have increased anyway without reducing bear numbers. Comparisons of calf:cow ratios in the area where moose calf survival significantly improved following the bear transplant in 1979 illustrate this point. This area's bear population was probably reduced proportionately more than other areas; however, calf:cow ratios appeared fairly stable from 1980 through 1988 while the moose population increased, as evidenced by moose observed/hour of survey (Fig. 1). There are >4 possible explanations for apparent lack of improvement in moose calf survival (Miller and Ballard 1992): 1. The moose population was nearing carrying capacity and bear predation became more compensatory to other mortality factors; 2. The wolf population increased while bear reductions were in progress and thus the calves "saved" by reducing bears were now being killed by wolves; 3. Sex-age composition survey data were too variable to detect slow increases; and 4. Other unknown factors, or some combination of

factors negated the effects of reduced bear densities. As a result of these findings, Miller and Ballard (1992) cautioned moose managers not to routinely liberalize bear hunting regulations with the express purpose of increasing moose calf survival.

Quebec

Crete and Jolicoeur (1987) tested the hypothesis that wolves and black bears were keeping the moose population below habitat carrying capacity. They reasoned that moose calf survival and density should increase if predator populations were significantly reduced. They manipulated wolf densities in 1 area, black bears in another, and examined 1 area with no predator manipulation.

Moose densities in the study areas appeared to level off at 400-500 moose/1,000 km² in the absence of hunting. Removal programs reduced wolf density from 21 to 8-11 wolves/1,000 km², while wolf density in the unmanipulated area ranged from 8-15/1,000 km². Black bear density prior to control

MOOSE COUNT AREA 3 - GMU 13 CALVES/100 COWS & MOOSE OBSERVED

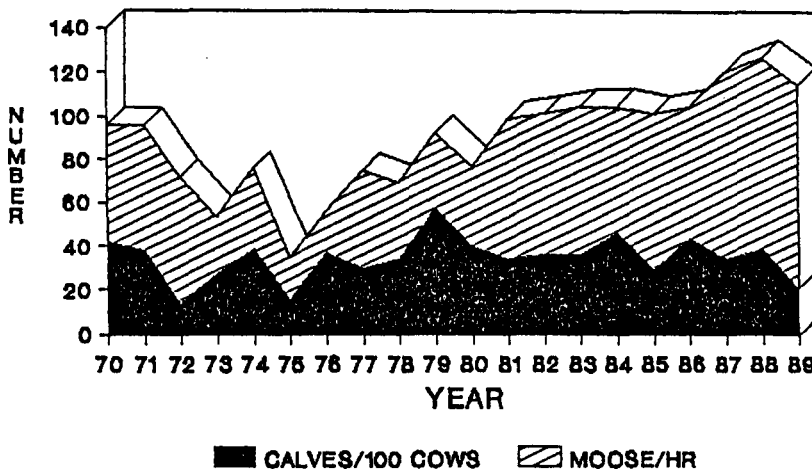


Fig. 1. Moose observed per hour of survey and ratios of calves: 100 cows observed during autumn surveys within Moose Count Area 3 from 1970 through 1989 within southcentral Alaska. (Wolves were controlled during 1976-78 and grizzly bears were transplanted from the area in 1979 [see text, Ballard *et al.* 1987, Miller and Ballard 1982]).

was estimated at 230/1,000 km² but may have been as high as 300-400/1,000 km². They removed 25-30 bears/year resulting in a harvest density removal of 70/1,000 km² or about 20-30% of the bear population.

There were 80 calves:100 cows in the wolf removal area and the unmanipulated area following treatment. Calf:cow ratios in the bear removal area were higher (110:100) than in the other 2 areas, but the differences were not statistically significant (Crete and Jolicoeur 1987). They concluded that the lack of statistical differences was due to insufficient reductions of predator populations, annual and regional variations among study areas, sampling error, small sample sizes, and proximate small study areas.

Messier and Crete (1985) had earlier questioned whether black bear predation on moose was density dependent. Crete and Jolicoeur (1987) stated that the improved calf moose survival seemed proportional to the number of bears killed/10 km² rather than to the numbers of bears removed per moose, thereby indicating that bear predation is not density dependent.

Saskatchewan

Stewart *et al.* (1985) reported that the moose population in the 1970's in eastcentral Saskatchewan exhibited characteristics similar to those elsewhere in North America where predation was suspected of limiting moose population growth. Calf:cow ratios in early winter declined from 60-80 calves:100 cows in mid 1970's to 30-40:100 in late 1970's and early 1980's. Moose studies indicated that most cows were producing calves, but only 32calves:100 cows were present by September (Kowal and Runge 1981).

Six of 12 radio-collared calves were killed by black bears in Saskatchewan (Beaulieu 1984). Consequently, they selected 2 study areas (Area 1-90 km² and Area 2-130 km²) to test the hypothesis that predation by black bears was limiting the moose population. They

attempted to remove all bears from each area for only 1 year (Area 1 in 1983 and Area 2 in 1984). Removal of black bears resulted in density estimates of 130 and 180 bears/1,000 km², respectively. Moose calf:cow ratios from bear removal areas were compared with ratios in unmanipulated areas.

Moose calf:cow ratios in the bear removal area were about twice as large as those in the unmanipulated areas during 1983 and 1984; 80 and 87 calves per 100 cows in bear removal areas versus 40 and 39 calves per 100 cows in unmanipulated areas for Areas 1 and 2 during 1983 and 1984, respectively. In the following year when no bears were removed, calf:cow ratios declined in each area and were not different from unmanipulated areas. However, the proportions of yearlings in the herd increased from 5-24% following the reduction, suggesting high survival of the improved cohort.

Stewart *et al.* (1985) suggested that the bear removal programs did not provide lasting relief from predation because calf:cow ratios declined the following year when bear removal ceased. However, because of the large improved calf cohort entering the yearling age class, calf:cow ratios would be expected to temporarily decline below the initial high levels but remain above precontrol levels for a 1-2 year period until the improved cohorts reach productive age classes and then ratios should continue to increase (Miller and Ballard 1992).

Based on bear removal rates, Stewart *et al.* (1985) estimated that black bears had been killing 40-48% of the moose calves in their study areas. Where high density black bear populations had been heavily hunted, moose calf:100 cow ratios were as high as 60-80 calves/100 cows during early winter surveys (Stewart *et al.* 1985).

DISCUSSION

Moose calf mortality studies have now been conducted in 7 geographic areas within

at least 10 different study areas of North America. In all, predation by grizzly or black bears has been the most important source of mortality (Table 1). Calf mortality rates due to grizzly bear predation have ranged from 2.7-52.2%, with the lower rates associated with relatively low grizzly bear densities (12/1,000 km²) and when black bears have been 10 times more numerous. Mortality rates from black bear predation have ranged from 2-50% when bear densities range from 16-570/1000 km².

Moose calf mortality attributable to wolf predation has been relatively low (i.e., <18%) in relation to that caused by grizzly bears in the 10 study areas (Table 1). Spring wolf densities in these areas have ranged from 1.8-5.9/1,000 km². These low rates of mortality due to wolf predation appear to contradict the projected impacts derived by other types of data. For example, significant ($P < 0.05$) correlations between spring wolf densities and subsequent autumn moose calf:cow ratios in southcentral Alaska (Ballard *et al.* 1987) suggested that wolf predation accounted for a larger percentage of the calf mortality than indicated by collared calf survival data (Table 1). Wolf scats collected from den and rendezvous sites in that area suggested that about 35% of the biomass of the wolf's diet during that time period was composed of calf moose. Extrapolation of the latter estimate to the moose population suggested that wolves were annually killing 3.4 to 8.9% of the moose calves born (Ballard 1992). Also, aerial observations of radio-collared wolf packs indicated that 30% of the classified moose kills during May and June were composed of calf moose (Ballard *et al.* 1987). Similar discrepancies also occurred in the Yukon Territory (D. G. Larsen, Yukon Dep. Renewable Resources, pers. commun.). Based upon the above observations I speculate that the low incidence of mortality due to wolf predation may be due to wolves avoiding radio-collared moose calves, small sample sizes, sampling

error, or other unknown factors.

Grizzly bears appear to become significant causes of calf moose mortality when bear densities are >16/1,000 km² even when black bears and wolves occur at similar densities (Table 1). They also can be a significant source of adult moose mortality (Boertje *et al.* 1988; Ballard *et al.* 1990, 1991; Larsen *et al.* 1989), but additional studies are needed to clarify relationships. Black bears, on the other hand, can be a significant cause of calf moose mortality when they greatly outnumber grizzly bears and/or wolves by at least a factor of 10 or when they are the only bear species present or their densities are >200/1,000 km² (Table 1). They are not effective predators when they outnumber grizzlies by a factor of 4 or wolf numbers by a factor of 30. They are not important predators of adult moose. Predation by either of the 2 bear species does not appear to be proportional to bear density (Ballard *et al.* 1990).

All moose calf mortality studies conducted thus far have found no differences ($P > 0.05$) in mortality rates by sex or between single and twin calves (Ballard *et al.* 1991, Boertje *et al.* 1987, Franzmann and Schwartz 1986, Larsen *et al.* 1989a, and Schwartz and Franzmann 1991). Capture induced-mortalities, usually from abandonment, have averaged 9.2% (range = 2-28% [Livezey 1990]). Capture-induced mortality rates have been lowered by reducing handling time, using sterilized gloves and collars, and by reducing disturbance as much as possible (Ballard *et al.* 1979, Boertje *et al.* 1987, Larsen and Gauthier 1989, Livezey 1990). Excluding capture related mortalities, there have been no significant differences ($P > 0.05$) in timing of mortality and mortality rates between collared and uncollared moose calves suggesting that collaring did not predispose the calves to death (Ballard *et al.* 1981, 1991; Larsen and Gauthier 1989; Larsen *et al.* 1989).

In studies where predation from grizzly bears has been the largest cause of mortality

all investigators have classified such mortality as additive. Grizzly bear and moose densities in such studies have ranged from 10-28 and 175-900/1,000 km², respectively (Table 1). Predation by black bears and wolves in the latter studies may have been partially compensatory. In studies where black bears have been the largest cause of moose calf mortality, both bear and moose densities have been high, i. e. 200-570 and 500-3,700/1,000 km², respectively (Table 1). On the Kenai Peninsula, Alaska, black bears were nearly 10 times more dense than grizzly bears and moose densities ranged from 1,000 to 3,700 km². In that case predation by black bears was probably a compensatory form of mortality because a moderate number of calves survived during spring through autumn only to die of starvation during winter (Schwartz and Franzmann 1990). In Saskatchewan where moose densities were lower (i.e. 450/1,000 km²), predation by black bears was probably an additive form of mortality because annual calf survival increased for the short term following reductions in bear densities (Stewart *et al.* 1985).

Schwartz and Franzmann (1990) suggested that predation and habitat quality operate in concert to control moose numbers on the Kenai Peninsula, Alaska. Such mortality acts in a compensatory or additive fashion depending upon habitat quality, predator density, or winter weather. They proposed that moose rates of increase and decrease and absolute density were influenced by predator densities similar to those in other North American studies (Ballard and Larsen 1987, Crete 1987, Gasaway *et al.* 1983).

Several biologists have suggested that mortality is increasingly compensatory as ungulates approach habitat carrying capacity but additive when populations are at low densities (McCullough 1979, 1984; Crete 1987; Gasaway *et al.* 1990). Predation from black bears is largely compensatory in areas where high density moose populations are

near habitat carrying capacity, such as the Kenai Peninsula, Alaska. An increasing proportion of predation from bears is additive in many other areas of North America as moose densities decline below 700/1,000 km². Bear predation may be totally additive at low moose densities (i.e., 175/1,000 km²) such as in eastcentral Alaska.

There appeared to be an inverse relationship between causes of mortality due to grizzly bear predation with moose density (Table 1). Comparisons of grizzly bear predation rates with moose densities from 3 studies suggests that predation rates were not related to moose density. The former relationships included all studies where grizzly and black bear populations occur sympatrically and where relatively reliable estimates of both bear and moose density have been reported. These relationships suggest that predation from grizzly bears can have a disproportionately greater impact on low versus high density moose populations.

Comparison of calf mortality due to black bear predation with moose densities suggests no relationship between moose density and mortality (Table 1). Predation rates by black bears on moose calves in 3 studies appeared related to moose density.

Theories of Population Regulation and Limitation.

Where moose constitute the principal prey species in multiple predator ecosystems containing wolves and 1 or 2 bear species, moose populations can be limited at low densities for decades. This theoretical model is referred to as the low density equilibrium model (LDEM) and has been proposed by Messier and Crete (1985), Crete (1987, 1989), Van Ballenberghe (1987), Bergerud and Snider (1988), and Gasaway *et al.* (1990). Based upon the findings of Boertje *et al.* (1988) and Ballard *et al.* (1990) that grizzly bear predation rates were independent of moose densities, Gasaway *et al.* (1990) suggested that such density-inde-

pendent processes could be a major factor in determining the set point equilibrium and relative range of moose densities.

There does not appear to be any regulatory feed-back between bear and moose populations and thus moose populations limited by bear predation could remain at low densities for extended time periods. Removing or reducing bear predations in some situations may allow moose populations to stabilize at higher densities through density-dependent processes.

Van Ballenberghe (1987) suggested that moose populations which are preyed upon by single species such as wolves (or perhaps bears), where alternate prey are scarce, tend to undergo what he termed recurrent fluctuations. He stated that an important distinction between recurrent fluctuations and low density equilibriums are that moose in the former may periodically escape predation, while those in the latter are held at low densities for long periods.

Results of all moose calf mortality studies indicate that bear predation is a significant cause of calf moose mortality. Bear predation can obviously be an important population limiting factor. Evidence collected thus far suggests that bear predation may not be a regulatory factor.

Management Implications

Moose populations limited by predation may increase dramatically when bear populations are reduced. The response of a moose population to predator removal depends upon the moose populations relationship to habitat carrying capacity and the distribution and densities of other predator species. In southcentral Alaska a temporary 60% reduction in grizzly bear densities accompanied by low wolf densities and mild winter conditions resulted in significant short term improvements in moose calf survival (Ballard and Miller 1990). Whether smaller reductions in bear numbers would increase calf survival

proportionately and when such mortality changes from largely additive to compensatory mortality is not known. However, a 36% reduction in grizzly bear numbers over a 7 year period with moose densities approaching 775-925/1,000 km² (Miller and Ballard 1992) failed to improve moose calf survival. A number of potential explanations exist for the lack of increase (*see* Bear Removal Programs - Southcentral Alaska), but no conclusive evidence is available. Although bear reduction programs may be helpful in elevating low density moose populations, they may not be necessary or worthwhile in moderate density moose populations (i.e., southcentral Alaska).

When moose populations are limited at low densities due to grizzly bear predation I speculate that large (>50% density) reductions may be necessary to achieve measurable increases in moose calf survival. No differences in grizzly bear predation rates on calf moose by sex, age, or family status of bear, lack of a relationship between moose densities and bear predation rates, and the facultative nature of bear predation suggests that large reductions in bear numbers would be necessary to achieve elevated moose densities.

In addressing declining moose populations, Ballard *et al* (1991) suggested that any management action should satisfy 2 important criteria: (1) high likelihood of attaining the immediate objective, and (2) side effects which are predictable, easily measurable, moderate in magnitude, of short duration, and easily reversible. Management options can involve no action, reducing human harvest, reducing bear densities, reducing wolf densities, or various combinations. Because grizzly bears have been eliminated from more than half of their range in North America, and because of their low reproductive rates, relatively low densities, and the difficulty of detecting and/or managing changes in bear populations, I recommend that managers not routinely manipulate grizzly bear populations to improve moose calf survival. Until prop-

erly conducted research programs provide managers with guidelines for managing bear-moose relationships purposeful reductions in bear numbers should only occur as part of well-designed research programs aimed at clarifying important ecological relationships. If predators must be managed, managers should first focus their efforts on black bears and/or wolves which have higher reproductive rates and consequently greater rates of population increase. Such populations are more forgiving of mistakes and can rebound quickly so long as adequate habitats are provided.

Ballard and Larsen (1987) and Van Ballenberghe (1987) at the Second Moose Symposium advocated additional and continued long-term research concerning bear-moose relationships. There are now fewer ongoing studies of bear-moose relationships than there were in 1984. The relatively low number of studies contained within this review suggest we barely have scratched the surface of understanding much less managing multiple species predator-prey interactions.

SUMMARY

Grizzly bears become significant sources of moose calf mortality when their density exceed 16/1,000 km². Black bears are a significant source of mortality when they outnumber grizzly bears and wolves by factors of 10 and 30, respectively or their densities are >200/1,000 km². Mortality due to bear predation can be compensatory or additive depending upon the moose populations relationship to vegetative carrying capacity. Causes of moose calf mortality are not proportional to either bear or moose densities. Rates of predation by black bears appear to increase with moose density. There does not appear to a relationship between grizzly bear predation rates and moose density. Predation by black or grizzly bears usually in conjunction with wolf predation can limit moose population growth. Insufficient data exists to evaluate whether bears can regulate moose populations.

Once bear predation has been identified as the primary limiting factor managers may have relatively few options unless they are willing to greatly reduce bear densities.

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