MOOSE POPULATION RESEARCH AND MANAGEMENT STUDIES IN YUKON

CAUSES AND RATES OF MOOSE MORTALITY IN THE SOUTHWEST YUKON 1983-1985

by
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CAUSES AND RATE OF MOOSE MORTALITY IN THE SOUTHWEST YUKON, 1983-1985

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ABSTRACT

The role of grizzly bears (Ursus arctos), wolves (Canis lupus), black bears (Ursus americanus) and humans in affecting moose (Alces alces) numbers in a 6310 km^2 area in the southwest Yukon was studied during 1983-85. Wolf numbers were reduced during the course of this study. Pregnancy rates, birth rates, and causes and rates of natural mortality were documented for radio-collared cows. Pregnancy, birth and twinning rates were estimated as 84%, 114 calves/100 cows, and 28% respectively. The mean annual survival rate of adult cows was 91% with the majority of deaths occurring during May - October. Grizzly bears were the primary and wolves the secondary cause of adult moose mortality based on information from radio-collared cows. Of all calf deaths occurring from known causes, predators accounted for 92%, of which grizzly bears were the main cause (58%), followed by wolves (25%). Grizzly bears were a more effective predator of moose calves compared to wolves between birth and 20 June. After 20 June, wolves killed proportionately more calves than grizzly bears. The average annual rate of calf survival was 25%. Of the calves that died (N=72), 82% died by 15 July and 90% by 1 November. No significant ($p > .05$) difference was found between the time of birth (early, peak or late born), and the number of days that the calf survived. Similarly, no difference was found in calf survivorship as related to the age of the cow or the sex of the calf. Grizzly bears accounted for 50%, wolves 26%, and licenced hunters 9% of all adult and calf mortalities over one year. We suggest that predation, primarily by grizzly bears and secondarily by wolves, was limiting the growth of this moose population. The management implications of these findings are discussed.

INTRODUCTION

The demand for moose by Yukoners for subsistence and sport hunting is the highest of all big game species in the Yukon. This demand is focused in the southwest Yukon where approximately 30% of both the resident harvest and hunting effort are concentrated in 4% of the land area. In addition, the nonconsumptive use of this resource is also focused, with the Yukon's human population concentrated (75%), and a major tourist transportation corridor (Alaska Highway) located in the southwest Yukon.

As a result of this intensive use, a comprehensive understanding of the moose population status and the factors limiting population size were required in order to effectively manage this resource. Fall aerial surveys in 1981, 1982 and 1983 (Larsen 1982, Johnston and McLeod 1983, Johnston et al 1984, Markel and Larsen 1984) indicated the population was stable at a density of 190-250 moose/1000 km^2 with low calf/cow (18-30/100) and yearling/cow (4-22/100) ratios. Neonatal calf mortality to 6 months of age was estimated to be between 80-86% in 1981 (Larsen 1982).

Predation was suspected to be the primary cause of low moose calf survivorship and the principal limiting factor to population growth, based on demographic characteristics of this population and recent studies conducted on moose predator systems throughout North America, as reviewed by Ballard and Larsen (1988). Both indirect and direct methods have been used to identify predation by wolves, grizzly bears and black bears as significant proximate causes of moose mortality. Indirect methods have included studies of: 1) predator kill rates combined with moose/predator ratios (Fuller and Keith 1980, Bergerud et al. 1983, Messier and Crete 1985), and 2) increased calf/cow ratios and/or increased moose population growth rates in response to predator reduction

(Ballard et al. 1981, Gasaway et al. 1983, Stewart et al.1985). Direct measures of the causes and rates of mortality has been made possible through radio-collaring (Franzmann et al. 1980, Ballard et al. 1981, Gasaway et al. 1983, 1986b). This study was designed to directly assess the dominant proximate causes of calf and adult female moose mortality through radio telemetry methods from 1983 through 1985 in the southwest Yukon.

Although predation has been identified as a major source of moose mortality, its importance as a limiting factor to population growth has been more difficult to discern (Connolly 1978). In this paper we address the question of limitation by identifying the major known causes of mortality (natural and hunting) on the moose population over 1 biological year, and assessing their relative importance.

STUDY AREA

The study area (6,310 km^2) was located adjacent to the British Columbia-Yukon border (Fig. 1). The physiography was characterized by rugged mountains with shallow valleys. Alpine and subalpine habitats were extensive, with 76% of the area above treeline (1,200 m). Thirty percent of the study area was considered unsuitable moose habitat (i.e. precipitous slopes, icefields, rocky areas above 1,500 m and large water bodies) (Larsen 1982). The vegetation reflects differences in physiography, weather, and fire history. Lichens and graminoids occur on lower exposed alpine slopes, and shrub birch (*Betula* spp.) and willows (*Salix* spp.) colonize subalpine and lowland riparian habitats. Scattered white spruce (*Picea glauca*) dominate lower subalpine elevations and extend into valley bottoms where lodge-pole pine (*Pinus contorta*) were prevalent. Paper birch (*Betula papyrifera*) and poplar (*Populus* spp.) were scattered throughout valley floors. Forest fires have been suppressed in this area for at least the past two decades. The climate was cool and dry. The 30 year mean annual temperature and precipitation at Whitehorse was $-1.2^{0}C$ and 261mm, respectively. Snow accumulation averaged 67cm. During this study, temperature, precipitation and snow accumulation were similar to the long term average. The physiography, climate and vegetation of this area have been described in more detail by Oswald and Senyk (1972) and Davies et al. (1983).

Wolf, grizzly bear and black bear were the major predators inhabiting the study area. Mid-winter wolf densities in 1982 were approximately 13 wolves/1,000 km^2 of total land area (Hayes et al. 1985). Wolf numbers were reduced from an estimated 74 animals in the fall of 1982 to 37 (50% reduction) by late winter, prior to the beginning of the moose mortality study in 1983. The wolf population subsequently rebuilt to near pre-reduction levels with 63 wolves in the fall of 1983, and was further reduced to 35 (44%) by March 1984 (Hayes and Baer 1986). A population of 54 wolves in the fall of 1984 was reduced to 14 (74%) by March 1985 (Hayes and Baer, in prep.). Reductions prior to 1983 likely did not effect moose survival rates, as the majority of wolves were removed around the northern and eastern periphery of the study area (Hayes et al. 1985) and the majority of the collared moose were in the central and western portions of the study area. Reductions in 1984 and 1985 potentially affected moose survivorship. Larsen and Markel (in prep.) estimated 16 grizzly bears/1000 km^2 of total land area in the study area in 1985. One grizzly bear was harvested in 1983, 8 in 1984 and 10 in 1985. These rates likely had minimal effect on the bear population and thus on moose survival rates. Black bear populations occur sporadically in forests and subalpine habitats. Densities were unknown, but thought to be similar to grizzly bear densities.

Dall's sheep (Ovis dalli) were the most abundant ungulate in the study area (300/1,000 km^2 total land area) (Barichello, pers. comm.). Caribou (Rangifer tarandus) densities have been estimated at 22/1,000 km^2 total land area (Farnell, pers. comm.). Snowshoe hare (Lepus americanus) numbers were low throughout the Yukon in 1983 (Slough 1984), at densities of 20 hares/1,000 km^2 in southwest Yukon (Boutin et al. 1986, Ward and Krebs 1985). Beaver (Castor canadensis) were common (3-12 km of stream/active colony) in the northeast corner of the study area (Slough and Jessup 1984), but likely uncommon in the remainder of the study area, based on physiography and available habitat.

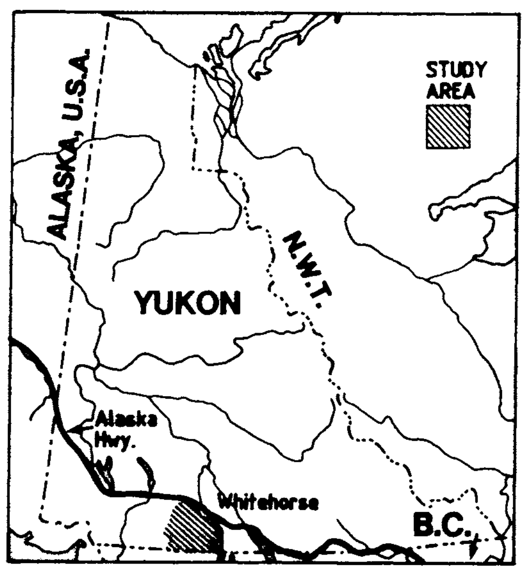

Figure 1. Southwest Yukon Territory Study Area.

METHODS

Estimating adult cow parameters

Thirty-nine cow moose ≥22 months of age were captured in March 1983 and 5 in March 1984. All broad habitat types which moose occupy in this area were searched and all moose were located and captured from a helicopter. Animals were captured as they were encountered, thus minimizing potential biases due to age, reproductive status and habitat use. Moose were immobilized with various combinations of carfentanil (Janssen Pharmaceutical, Mississauga, Ontario), xylazine hydrochloride (Rompun: Cutter Laboratories), fentanyl citrate (Janssen Pharmaceutical) and hyaluronidase. Dosages of carfentanil varied from 2.0 - 3.2 mg/cow. Fentanyl citrate and hyaluronidase when administered, were given at 30 mg/cow and 150 mg/cow,respectively. Xylazine was administered at either 40 or 50 mg/cow. The drug was administered from a Cap Chur dart gun (Palmer Chemical and Equipment Co., Douglassville, Georgia). One hundred and twenty to 220 mg of naloxone per cow (E.I. du Pont de Nemoirs, Glenolden, Pennsylvania) and 1 to 4 mg/cow of diprenorphine (M50:50; Cyanamid, Montreal, Quebec) were used as the narcotic antagonists.

Age was determined by tooth-cementum annuli from incisors (Sergeant and Pimlott 1959, Gasaway et al. 1978) of 43 cows. Pregnancy was determined through rectal palpation (Arthur 1964, Haigh et al. 1982) of 43 cows during March-April of 1983 and 1984. Timing of birth and the number of calves born was determined through daily visual monitoring of radio-collared cows during the 1983 and 1985 calving periods. The causes and rate of adult cow mortality were estimated for 33 radio-collared cows in 1983, 34 in 1984 and 41 in 1985. Calves which were collared in 1983 and still alive in May 1985 were included in the adult mortality estimate in 1985/86. Collars with 6-hour mortality switches were used (Telonics, Mesa, Arizona), and all immobilized moose were monitored within 48 hours of administering the antagonist to identify capture-related deaths. Cows accompanied by a calf were monitored daily from mid-May through mid-July in 1983 and 1985, and weekly in 1984. Cows were located 1-2 times/month during the remainder of 1983/84 and 1984/85. In 1985/86 cows were monitored once in September, November and April. Survival rates of adult cows were estimated by dividing the number of cows collared at time t and still alive at time t + 1 by the number of collared cows at time t. Three intervals were used: (1) 12 month annual period (17 May-16 May); (2) 6 month snow-free period (17 May - 1 November); and (3) 6 month snow period (2 November - 16 May). The 17 May date was used as the beginning of a biological year as it corresponded to the start of calving, and allowed for consistency between cow and calf periods. Only cow moose monitored throughout an entire biological year were used in calculating survival rates. The cause(s) of mortality was determined by evidence at the mortality site (Gauthier and Larsen 1986); however, the identity of predators was not determined for mortalities occurring between mid-July 1985 and May 1986 due to the infrequent level of monitoring.

Estimating calf parameters

Two types of calf/cow groups, based on collar status, were used in this study: 1) collared calves with collared cows (group 1, N=40) and 2) collared calves with uncollared cows (group 2, N=79). Sixty newborn calves were collared in 1983 and 59 in 1985. Calves were located from a helicopter during daily monitoring flights, physically restrained, and collared after the helicopter had separated the calf from the cow (Larsen and Gauthier 1986). Expandable/breakaway collars (Schlegel 1976) were used on transmitters equipped with 2-hour mortality switches (Telonics, Mesa, Arizona).

The ages of all collared calves were estimated at the time of collaring to evaluate whether or not all potential postpartum mortality was being measured, and to determine parturition dates. The ages of calves with collared cows were determined from daily monitoring flights of the cows. The ages of calves with uncollared cows were based on the following characteristics which were observed in calves of known age: 1) a calf $<$ 1-day old was unable to stand, or was unsteady on its feet, or the umbilical cord was still attached, or the calf was still wet; 2) a 1-day old calf was steady on its feet, or slowly walked towards the field crew, or attempted to follow the cow; 3) a 2-day old calf walked quickly after the cow when approached by the field crew, and 4) a 3 to 7-day old calf ran after the cow when approached but could still be caught by the field crew. Calves which were too mobile to be captured on the ground were judged to be $>$ 1-week old. Birth dates were determined by back-dating from the estimated age of the calf at collaring. Male and female calves were distinguished in 1985.

The proximate causes of mortality of collared calves (N=119) were determined in 1983 and 1985, and differences between years were tested. All mortalities were investigated immediately upon receiving a mortality signal. When a mortality signal was detected, the helicopter descended to between 50m and 150m above ground level and an area within approximately 1km of the mortality site was searched for predators. Dead calves were subsequently examined and cause of death was determined by the presence of sign at the mortality site. We believe that the predator assigned to a calf mortality was the proximate cause of death as opposed to a scavenger. (Gauthier and Larsen 1986).

Causes of mortality were initially classified as 1) grizzly bear, 2) wolf, 3) black bear, 4) grizzly bear/wolf, 5) grizzly bear/black bear, 6) predator unknown, and 7) non-predator causes (e.g. drowning). The dual predator groups

(4 and 5), consisting of 8 of the 81 mortalities, were divided among the single predator-groups according to their relative proportions.

In 1983 grizzly bears observed on calf carcasses were classified as either females with offspring (cubs of the year, yearlings or 2 year olds) or adult bears of unknown sex. In 1985 bears found on carcasses were immobilized and classified according to sex and age (Larsen and Markel in prep.).

Due to the frequency of monitoring calves during the first 6 weeks after parturition, mortalities were likely investigated within 12 hours of death. In 1983, calves were monitored from either a helicopter or fixed-wing aircraft 1-4 times/day from birth to the end of June, weekly through July, 2/month to December and 1/month to May. In 1985, calves were monitored 1-4 times/day between birth and the end of June, daily to July 15 and once in September, October, November and March. If more than 1 week lapsed between calf relocations, a cause(s) of mortality was not assigned, with the exception of cases (N=7) where a single predator species could be identified from adequate sign left at the kill site.

The rate of calf survival was determined from collared calves with uncollared cows (N=39) in 1983 and from collared calves with both collared and uncollared cows (N=57) in 1985. Calves of collared cows were excluded from the 1983 analysis due to the negative effects of immobilizing cows on post-natal calf survivorship in this study area (Larsen and Gauthier 1986). This effect was only detected in the year the cow was immobilized, therefore, calves of cows immobilized in 1983 and 1984 were used to estimate calf survival rates in 1985.

Survival rates were estimated for 4 intervals: (1) 17 May - 20 June (calving); (2) 21 June - 1 November (post-calving/summer); (3) 2 November - 16 May (winter); and (4) 17 May - 16 May (annual). Only calves with which radio contact was maintained throughout a complete interval were used to estimate calf survival, following the same technique described for cows.

A second measure of calf survival for the period May to November 1983 was made by comparing the estimated number of calves in a November 1983 aerial census to the number of calves predicted to be born in the same year. The number of calves born was predicted by multiplying the number of adult females at calving 1983 (estimated from a 1983 fall census and corrected for summer mortality) by the average (1983 and 1985) birth rate. Moose population size and composition were estimated for the study area using a stratified random block sampling technique described by Gasaway et al. (1986a) and modified for Yukon terrain and climatic conditions by Larsen (1982).

The effects of some potential biases on calf survivorship were investigated. Birth period (early born 17-22 May, peak born 23-29 May, and late born 30 May - 9 June), and cow age (inexperienced 1-5 years; experienced 6-9 years; and old 10-15 years) were assessed by comparing calf duration (number of days between birth and death) to birth period, and calf survivorship status (alive or dead) after 1-year to cow age. Calf survivorship by sex was assessed by comparing calf status after 1-year to the sex of the calf. The effects of drugging pregnant cows on pre and postnatal calf survivorship and the effects of handling and collaring calves on postnatal calf survivorship were reported by Larsen and Gauthier (1986).

Estimating Moose population and hunting status.

In order to evaluate the relative significance of the various causes of mortality, we estimated the size and composition of the moose population, the number of deaths, and the causes of mortality over a 1-year period. This evaluation was made for the May 1983 to May 1984 time period. The size and composition of the population was based on a November 1983 post-hunt aerial census. The 1983 pre-calving adult population was estimated by adding the natural and hunting mortalities from the summer period to the November 1983 adult population. The 1984 pre-calving population was estimated by subtracting the winter mortality from the 1983 fall population estimate. In both extrapolations, we assumed the causes and rate of adult male and yearling natural mortality were equal to that measured for radio-collared adult cows.

The annual harvest of adults and calves was determined through a hunter questionnaire for residents (Kale 1982) and through compulsory registration for non-residents. Harvest figures reflect minimum values as no estimates were available for non-licenced native hunters.

Analysis.

Statistical differences between means were determined by t-test analysis and differences in proportions by log-likelihood ratio analysis. Unbalanced ANOVA analyses were used to test for differences among multiple parameters. An alpha level of 0.05 was used to determine significance.

RESULTS AND DISCUSSION

Productivity and natural mortality of adult cows.

Productivity of adult cows ≥24 months in the study area was considered good. Thirty-six (84%) of the 43 cows diagnosed were pregnant and the average (1983-85) birth rate (calves born/pregnant and non-pregnant cow, N=65) was 114 calves/100 cows. Twins were observed with 16 (28%) of the 58 collared cows with calves. The mean age of cows was 8 years (SE=0.5).

Predation was the major cause of adult cow mortality. Ten (23%) of 43 collared cows died over the 3-year period from 1983 through 1985. Thirty percent died from unknown causes, grizzly bears accounted for 30%, wolves 20%, grizzly bears or wolves 10%, and unknown predators 10% (Table 1). Based on this limited sample, grizzly bears appeared to be the primary known natural cause of adult cow mortality during this study. These findings are supported by adult moose mortality and grizzly bear predation studies conducted in Alaska. Ballard et al. (1988) and Boertje et al. (1988) both reported significant levels of grizzly bear predation on adult moose. Grizzly bears were also a significant cause of adult cow mortality in eastcentral Alaska (Gasaway et al. 1986b).

Most adult cow mortalities occurred between May-November. The average annual survival rate of cows was 91% during the 3-year period (Table 2). Eight of the 10 mortalities occurred during the summer, yielding an average snow-free survival rate of 93%. Only 2 collared cows died during winter. Our results contrast those of Peterson (1977) and Peterson et al. (1984) who reported the majority of predation on adult moose occurred during winter and early spring. One possibility for this difference is the absence or low density of grizzly

Table 1. Causes and rates of annual mortality of collared moose cows in 1983, 1984 and 1985, southwest Yukon.

		1983/84	1984/85	1985/86	Combined
Captured/present[a]		39	34	41	114
Lost contact		4	0	0	4
Capture related deaths		2	0	0	2
Remaining:		33	34	41	108
Natural Mortality:					
Known causes	- grizzly	1	1	1	3
	wolf	2	0	0	2
	wolf/grizzly	1	0	0	1
	predator unknown	0	0	1	1
unknown causes		0	1	2	3
Total Mortality		4	2	4	10

[a] A total of 44 cows were captured; 39 in 1983 and 5 in 1984. Collared cows present in 1984/85 were the sum of the 29 remaining as of May 1984 (33-4) and the 5 collared in March 1984. Collared cows present in 1985/86 were the sum of the 32 remaining as of May 1985 and the 9 1983 collared calves (now classified as adults) which survived to May 1985.

bears in those studies. Another possibility may be the number of radio collared cows dying during winter in this study under-represented mortality of the general population. From wolf predation studies conducted in the same area (Hayes and Baer 1986) we estimated kill rates of 5.4 kg of moose/wolf/day from 2 radio-collared packs between February and April 1984. Based on an estimated 63 wolves between November 1983 and January 1984, and 35 wolves between February and April 1984, approximately 48,300 kg. of moose would have been consumed. Using moose composition and weight data from wolf kills (Hayes and Baer 1986) this represents 54 adult cow moose. The estimated cow population (N=598) in November 1983 was calculated for a comparable study area from Markel and Larsen (1984). Based on these results, approximately 9% of

Table 2. Survival rates of collared cows by time period between 1983-1985 in the southwest Yukon.

Period	1983	1984	1985	Combined
Summer (17 May - 1 November)	88% (29/33)	94% (32/34)	95% (39/41)	93% (100/108)
Winter (2 November - 16 May)	100% (29/29)	100% (32/32)	95% (37/39)	98% (98/100)
Annual (17 May - 16 May)	88% (29/33)	94% (32/34)	90% (37/41)	91% (98/108)

the cow population was killed by wolves during the winter in 1983/84. This is substantially greater than the 2% indicated from our radio-collared cows. We believe the true mortality rate was closer to 9%, and suspect the difference was due to the small sample of collared cows.

Grizzly bear predation on adult cows appeared to be concentrated during the calving period and on parous females. Although the sample size is small, all 3 cows that were killed by grizzly bears had calves and 1 of these was likely in labor. Two out of the 3 cows killed by grizzly bears died during the calving period (May 14 and June 5) and the third shortly after (June 25). This result is in agreement with a recent study in Alaska which demonstrated that grizzly bear predation rates on adult moose were highest during the spring (Boertje et al 1988). We speculate that pregnant cows were vulnerable to predation during calving due to a suspected decrease in cow mobility immediately prior to, during, and following birth; and due to their innate behavior to defend newborn calves.

Extent and causes of calf mortality

Calving occurred over a limited time period. In 1983 and 1985 calves were first observed on 17 May, and no further calving was noted after 10 June. The median calving date was 25 May with 72% of calves born over a 9-day (22 May - 30 May) period (Fig. 2). No difference was found in the mean calving date between years.

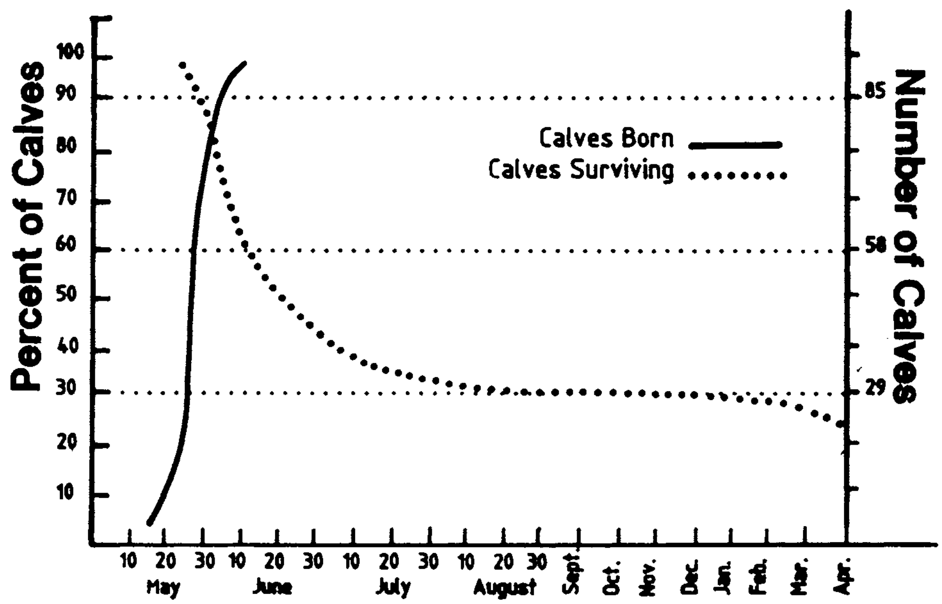

Figure 2. Timing of birth and death of radio-collared moose calves during 1983 and 1985, in the southwest Yukon.

Predators accounted for 77 out of 84 (92%) calf deaths from known causes in 1983 and 1985 combined (Table 3). No significant difference was found in the known causes of mortality between years or between calves with collared and uncollared cows, therefore data were combined. A higher proportion of unknown causes was recorded in 1985 as a result of less frequent monitoring after July 1985 as compared to 1983. For this reason only known causes were used for comparisons between years and combined totals. Grizzly bears were the major cause of annual calf mortality, accounting for 58% (49/84) of the known causes followed by wolves (25%) (Table 3).

Early neonatal mortality was detected as a result of the young age ($\bar{x}$=2 days, SE = $\pm$0.2) at which calves were collared. Of the 84 calf deaths, 27 (32%) occurred when the calf was <10 days old. Grizzly bears, either as a single or dual cause of mortality, accounted for the majority (67%) of these deaths. The major sources of mortality changed significantly approximately 1 month after the peak of calving. Between birth and 20 June, grizzly bears accounted for 60% of the calves that died and wolves 10%. After 20 June, wolves accounted for 54% and grizzlies 27% of the calves that died. We speculate that this shift may have been the result of a combination of factors including decreased vulnerability to bear predation due to increased mobility of calves (Ballard *et al.* 1980), decreased availability of calves after mid-June, or increased availability of an alternative food source (vegetation) for grizzly bears. The latest a collared calf was killed by a grizzly bear was August 4th. Studies in Alaska have also shown that grizzly bear predation on moose calves was highest during the first month after birth. (Ballard *et al.* 1981, 1988; Boertje *et al.* 1987, 1988).

Table 3. Causes of annual (May - May) mortality of collared moose calves (N=119) in 1983 and 1985, southwest Yukon.

			1983	1985	Combined
Captured:	collared		60	59	119
	capture related deaths		0	1	1
	lost contact		0	1	1
Remaining:			60	57	117
Natural Mortality:					
Known causes		- grizzly	34 (61%)	15 (38%)	49 (52%)
		- wolf	14 (25%)	7 (18%)	21 (22%)
		- black bear	1 (2%)	3 (8%)	4 (4%)
		- predator unknown	2 (3%)	1 (3%)	3 (3%)
		- non-predator (natural)	3 (5%)	4 (10%)	7 (7%)
Subtotal			54	30	84
Unknown causes			2 (3%)	9 (23%)	11 (12%)
Total			56 (100%)	39 (100%)	95(100%)

The causes of calf mortality results in this study are comparable to other moose calf mortality studies in areas where bears were abundant. Gasaway et al. (1986b) reported that in eastcentral Alaska, predators accounted for 23 of 27 (85%) radio-collared calf deaths over 1 year, and that grizzly bears were responsible for 17/27 (63%) of those mortalities. Franzmann et al. (1980) reported that black bears killed 34/53 (64%) calves that died from known causes prior to late summer on the Kenai Peninsula, Alaska. Ballard et al. (1981) estimated that grizzly bears killed 52/63 (83%) calves that died from known causes prior to November in the Nelchina Basin, Alaska. In order to compare our results with the above two studies conducted over the 6-month period after parturition, we have summarized our data for a similar time period. The known causes of calf mortality to 1 November for 1983 and 1985 combined were: predators 74/81 (91%); of which grizzly bears accounted for 49/81 (60%), wolves 18/81 (22%), black bear 4/81 (5%) and unknown predators 3/81 (4%).

Our data suggests that grizzly bears were the most effective predator on neonatal moose calves, even though 2 other predators (wolves and black bear) coexisted in the study area. During both the 1983 and 1985 calf mortality studies, grizzly bears and black bears were thought to occur at similar densities, yet grizzly bears accounted for 12 times the number of deaths. Ballard et al. (1988) reported similar findings from a predator-moose system in Alaska, where black bears outnumbered grizzly bears. They concluded, and we agree, that moose calf mortality was not directly proportional to the relative densities of the 2 bear species. Furthermore, grizzly bears and wolves were approximately equal in abundance in the central portion of our study area in 1983, yet grizzly bears accounted for 3 times the number of calf deaths to November. The results from these 2 studies suggest that grizzly bears are able to out-compete black bears and wolves for neonatal moose calves in northern multi-predator systems.

Our results also suggest that all age, sex and family bear groups killed moose calves. In 1983 and 1985, 12 bears or bear groups were observed feeding on calves. Seven (59%) of the 12 bears were females with offspring (2 with cubs of the year, 5 with either yearlings or 2-year-olds), 3 (25%) were males (2 7-years-old, 1 2-years-old), and the sex and age of the remaining two were unknown. Recent studies on grizzly bear predation rates on moose in Alaska (Ballard et al. 1988, Boertje et al. 1988) confirm that most bears prey on moose calves. Ballard et al. (1988) stated that predation rates on adult and calf moose varied, but not significantly between bear sexes, age groups and family classes. Differences were due to variability in predation rates by individual bears. Boertje et al. (1988) found no significant difference in predation rates on moose calves by the sex or reproductive class of bears and concluded that most, if not all, adult grizzly bears killed calves. Again, considerable variability in predation rates by individual bears was recorded. However, they did find that adult male grizzlies killed adult moose significantly more often than adult female bears. Large variability in predation rates by individual bears was reported but they concluded that the majority of adult male and some adult female bears kill adult moose.

Based on the number of neonatal calves killed in our study, we infer that most adult bears preyed on moose calves . We have estimated that 250 calves were killed by grizzlies in 1983 (Table 6). At a density of 16 bears/1000 km^2, with adults ($\geq$ 6 years) representing 49% of the population (Larsen and Markel, in prep.), approximately 49 adult bears would have potentially preyed on 250 calves for an average potential kill rate of 5.1 calves/adult bear. This value was similar to the 5.4 calves /adult bear (females $\geq$5 years and male $\geq$9 years) reported by Boertje et al. (1988) for eastcentral Alaska and the 5.3 calves/bear ($\geq$ 3 years) documented by Ballard et al. (1988) for southcentral Alaska. These consistent results suggest similarities in grizzly bear predation rates on moose calves over a wide geographical area.

Most calf mortalities occurred within 8 weeks of birth as demonstrated by the survival curve of 96 radio-collared calves from 1983 and 1985 (Figure 2). No significant difference was detected between annual survival rates (proportion of dead to alive calves) between years. Of the 96 collared calves, 44 (46%)

died by 20 June, 59 (61%) by 15 July, 65 (68%) by 1 November and 72 (75%) died by 1-year of age. This survival curve is similar in shape to that reported for other moose populations subject to heavy predation. Franzmann et al. (1980) and Gasaway et al. (1986b) documented 57% and 76% mortality of radio-collared calves within 10 and 8 weeks of birth, respectively. Ballard et al. (1981, 1988) reported a 55% and 82% mortality rate to 1 November, respectively.

Table 4. Survival rates of collared moose calves (N=96) by time period for 1983 and 1985, southwest Yukon.

Period	1983	1985	Combined
Calving (17 May-20 June)	41% (16/39)	63% (36/57)	54% (52/96)
Postcalving/summer (21 June-1 November)	56% (9/16)	61% (22/36)	60% (31/52)
Winter (2 November-16 May)	67% (6/9)	82% (18/22)	77% (24/31)
Annual (16 May-17 May)	15% (6/39)	32% (18/57)	25% (24/96)

Of the 72 calves that died in our study during their first year, 59 (82%) died by 15 July and 65 (90%) by 1 November. Ballard et al. (1981) documented similar losses (94%) by mid July.

Some potential biases affecting calf survival were tested: 1) We speculated that the relative time period of birth may affect calf survival, i.e. late born calves would have a better chance of surviving if: a) predators were saturated by the number of calves available during the early and peak born periods, or b) the primary predator (grizzly bear) switched from a meat to a vegetation diet over the calving period. However, no significant differences were found between the birth period of the calf and the number of days that it survived; 2) we also speculated that experienced cows were likely the best equipped, both physically and behaviorally, to defend their calves from predators. However, no difference was found in the proportion of dead to live calves in relation to the age class of the cow; and, 3) an equal proportion of male calves died compared to female calves in 1985, indicating that natural mortality was not selective, by sex of the calf, up to 1 year of age. In addition to these potential biases, the effects of collaring the calf on its survival were tested and found to be negligible (Larsen and Gauthier 1986).

Relative causes of adult and calf mortality

Grizzly bears were responsible for more deaths (natural and hunting) in this population (adults and calves), over 1 year, than any other single factor. The relative significance among the reported causes of moose mortality, and their contribution to the overall mortality in the 1983 population were determined by predicting the population size and composition at calving in 1983 and 1984 (Table 5). We estimated that between these calving periods 534 deaths occurred (412 calves and 75 adults and yearlings died from natural causes, and 47 adults and yearlings were killed by hunters). Of the 534 total mortalities, grizzly bears accounted for the majority of all deaths (50%), followed by wolves (26%), and hunting (9%) (Table 6). As noted earlier, winter predation on adult cows may have been underestimated in this study. Therefore, wolves may account for a higher percentage of the total annual moose mortality than shown in Table 6. Overall losses of adults to wolf predation however, would not exceed losses of calves to grizzly predation. Based on these results we conclude that predation by grizzly bears was both the dominant proximate cause of moose mortality and the major factor limiting moose population growth.

Without hunting, this population was stable as recruitment replaced natural mortality. Adult losses (75) from natural mortality (Table 6) were similar to the number of calves surviving (74) over one year (Table 5). However, with hunting, the population would decline. This is in spite of the fact that hunting represented a relatively small proportion of the overall deaths.

We conclude that the calf survival rates reported in this paper were a close estimate of the actual calf survival rates in the population. This conclusion was based, in part, on the agreement between the survival rate of calves to 6 months of age (23%) in 1983, as derived from population modeling (Table 5) and the survival rate derived from radio-collared calves (23%) (Table 4).

Table 5. Estimate of moose population size and composition between May 1983 and May 1984, southwest Yukon.

Estimated Composition	Estimated calving population 1983[a]	Estimated post-hunt fall population 1983[b]	Estimated calving population 1984[c]
Adult male	215	153	161
Adult female	426	371	379
Yearling male and female	20	16	74
Calf	486	111	431
Estimated population size	1147	651 ± 143[d]	1045

[a]Adult and yearling population estimates at calving 1983 were determined by applying the 1983 May- November natural survival rate (88%) documented for adult females to the adult and yearling cohorts (Table 2). Hunting losses occurred between August - November 1983 and comprised 41 adult males, 2 yearling males, 4 adult females. There are minimum values as the unlicenced native harvest was unknown. The losses due to hunting and natural mortality were added to determine the pre-calving populations. The estimated number of calves born was calculated by multiplying the predicted number of cows present at calving by the documented birth rate (114 calves/100 cows).

[b]Estimated from an aerial survey conducted in November 1983. (Markel and Larsen 1984).

[c]Calving 1984 population estimate was calculated from the over-winter survival rates of 67% for calves and 100% for adults. Fall 1983 yearlings which survived to calving 1984 were assumed to have an equal sex ratio and thus divided equally between the adult male and female groups.

[d]90% confidence intervals.

Table 6. Total annual moose mortality and the relative importance among causes (May 1983-May 1984), southwest Yukon.

Causes of mortality	Calves	Adults and yearlings	Combined N	Combined %
Grizzly	250	19	269	50
Wolf	103	37	140	26
Black Bear	7	0	7	1
Grizzly/Wolf	0	19	19	4
Predator unknown	15	0	15	3
Non-predator causes	22	0	22	4
Unknown causes	15	0	15	3
Hunting	0	47	47	9
Total	412[a]	122[b]	534	100

[a]Total calf deaths were determined by subtracting the estimated number of short yearlings at calving in 1984(74) from the estimated number of calves born in 1983 (486) (Table 5). This total was then divided among the various causes of mortality recorded in 1983 (Table 3).

[b]Total adult and yearling deaths were determined by subtracting the estimated number of adults at calving 1984 (540) from the estimated number of adults and yearlings at calving 1983 (661) (Table 5). This total (minus 47 hunting deaths) was then divided among the various causes of natural mortality recorded in 1983 (Table 1). Hunting deaths were added to the natural mortality.

MANAGEMENT IMPLICATIONS

These results have several implications for moose managers and researchers in areas with abundant predators, and in particular abundant grizzly bears. Over the past decade, studies on the rates or causes of moose mortality in North America (Franzmann et al. 1980; Ballard et al. 1981, 1984, 1988; Ballard and Larsen, 1988; Gasaway et al., 1986b; Stewart et al., 1985; present study) and studies on grizzly bear predation rates (Ballard et al. 1981, 1988; Boertje et al. 1988) have either documented or implied that grizzly bears or black bears are a significant cause of moose mortality and may limit population growth. Grizzly bears are also known to prey on moose in the U.S.S.R. (Danilov 1983) and Sweden (Haglund 1974). We recommend that research and management agencies planning to investigate moose limiting factors within areas where grizzly bears occur consider this predator to be a potential major source of moose calf and adult mortality. Grizzly bears may also be the most effective of the 3 northern predators (including wolves and black bears) on moose calves. If grizzly bears have a competitive edge over black bears and wolves, grizzly bears are potentially an important predator in areas where they occur at low densities.

This competitive behavior would confound the use of predator/prey ratios as a management tool to assess predator-prey relationships in multi-predator systems. Ungulate/predator ratios have been used in relatively simple predator-prey systems in the past to evaluate the importance of predation on a prey population (Mech 1966, Pimlott 1967, Gasaway et al. 1983). Managers may initially assess an area to be a simple predator-prey system based on the relative abundance of predators. However, if mortality is not directly proportional to the relative abundance of the predators, the use of simple ratios, in areas where bears occur, may be inappropriate. The results may lead to erroneous conclusions regarding the real effects of bears, or their relative importance, on moose calf survivorship and ultimately on the population. Ratios in our study area were 17 moose/wolf, 11 moose/grizzly bear and 7 moose/wolf and grizzly bear in 1983. Additional studies are needed to clarify the relationships between the number of prey and the number and type of predator in areas where more than one predator occurs.

We believe that the recent identification of grizzly bears as significant proximate causes of moose mortality was not a result of changes in bear feeding behavior but rather due to advances in radio-telemetry which allow direct identification of predators (Ballard and Larsen, 1988). In the past, bear scat analyses were used to infer predatory behavior and levels of predation. This indirect method of determining bear predation is open to several potential biases. A significant portion of the moose calf hide was not consumed by grizzly bears in the southwest Yukon (Gauthier and Larsen 1986) or in southcentral Alaska (Ballard et al. 1979) suggesting that the identification of moose calves in bear scats would be difficult. In cases where moose hair was present in bear scats, the tendency has been to assume that the calves were scavenged. In addition, bear predation on moose calves has occurred almost entirely within the first 6-8 weeks postpartum. Bear predation and its effects on the moose population would be underestimated if scats were not collected, or bear behavior not studied, during this short time period.

Managers should be aware of the relative significance of predation and hunting when managing for a sustained harvest. Population projections in this study indicated that the moose population would remain stable over the short term while subject to heavy predation, but would decline with the addition of hunting, although the latter represents a relatively small proportion of the overall mortality. This example demonstrates that few, if any, surplus moose exist for harvest in a system where major losses occur to natural predators. However, moose hunting is socially valued by many northern cultures (both native and non-native). As well, predators are likely abundant in most northern ecosystems. In order for moose hunting to continue, within sustained yield, management agencies must act responsibly by intensively managing these northern moose-predator systems.

Gasaway et al.(1983) suggests that managers have 3 options in most areas where predation limits growth of prey populations: (1) do nothing and allow the system to be naturally regulated (cycle); (2) allow the system to be naturally regulated and reduce or eliminate human harvest during prey declines; or (3) manipulate predator populations to enhance prey populations and thus maintain a sustainable harvest of prey. We suggest that predator reduction is the most practical short-term alternative to meeting human harvest demands for moose in northern multipredator systems. We also suggest that predator reduction programs should be accompanied by a reduction in moose harvest.

Without predator reduction, some moose populations will likely decline or remain at low densities for decades. Gasaway et al. (1983) suggested that fast acting feedback mechanisms which regulate predators relative to declining prey were lacking in some predator-prey systems. Loose regulatory feedback has been reported for wolf prey systems (Mech and Karns 1977, Peterson and Page 1983, Gasaway et al. 1983). Because the predator in these systems was an obligate carnivore, natural fluctuations in both predator and prey numbers would be expected, albeit infrequently. However, grizzly bears are not obligate carnivores and therefore any regulatory feedback between bears and moose would likely be insensitive and slow-acting (Ballard and Larsen, 1988; Ballard et al. 1984). Thus it may take decades for a moose population to escape control by bears in naturally regulated systems.

As moose densities decrease and bear densities remain stable, the effect of predation may increase, i.e. anti-regulatory control (Lidicker 1978; Gasaway et al. 1983; Boertje et al. 1988), thus forcing, and possibly holding, the moose population to even lower densities. It is important for managers to recognize this potential situation and take action to ensure that moose populations do not decline to low densities, or face decades with low moose numbers.

If the reduction of bear numbers was used as a management tool to increase moose populations it appears that numbers in all age and sex classes of bears will need to be reduced for the most effective results. Recent studies on grizzly bear predation rates (Ballard et al. 1988; Boertje et al. 1988) and the observations during this study suggest that most bears, (regardless of age, sex and family status) kill moose calves. Therefore, it would be an ineffective management strategy to selectively remove one specific bear class. Reducing adult moose mortality may be accomplished by removing large male grizzlies, however, the effect on the moose population would not be as significant as decreasing calf moose mortality by removing both adult male and female bears. As well, removing only adult male bears may increase bear recruitment (Young and Ruff 1982) as male grizzlies are effective predators on grizzly cubs (Reynolds and Hechtel 1984). Removing only adult male grizzlies could result in increased mortality to the moose population.

The effects of removing grizzly bears on calf survivorship may be confounded by intra and interspecific compensation in predation rates. A reduction in grizzly bear numbers would increase the availability of calves to wolves and black bears within the first 6-months post partum and to wolves later in the winter. Increased predation by other predators could negate the effects achieved from grizzly bear reduction. As well, a reduction in grizzly bear numbers could result in the remaining grizzly bears killing more calves. For these reasons, reduction programs that are designed to increase moose calf survivorship and thus moose populations in multi-predator systems should include actions to remove a portion of all major predators in the system.

Based on the above management ramifications, we recommend that a regional, multi-species management plan be developed to address the basic issue of management objectives. Without clearly defined and commonly held objectives, management strategies for moose and their predators will continue to be at odds. A key function of this plan would be to identify acceptable population levels for moose, grizzly bears and wolves. Once target levels and time frames have been identified, management strategies to achieve those levels can be implemented.

If current moose levels are acceptable from a public policy perspective, then the management objective would be to closely monitor the population to ensure population levels do not decline and that adult male to female sex ratios do not fall below 30:100. This minimum ratio was recommended by Larsen and Kale (1982) for the southern Yukon. Between 1981 and 1986 the average male:female ratio in this population was 33:100 (Larsen *et al*. in prep.). If a decline does occur, a management strategy to enhance population levels should be implemented immediately, before anti-regulatory control occurs.

This strategy should involve the concurrent reduction of grizzly bears, wolves and hunting. If the adult sex ratio drops below the minimum acceptable level, the harvest of male moose should be severely restricted. Current hunting levels (licenced and nonlicenced) should be kept within the sustained yield of the population to reduce the potential need for future predator control programs. In order to maintain a sustained yield and be able to detect population declines, we recommend an aerial census of this population be conducted every four years starting in 1989, followed by less intensive trend counts every second year.

If current moose levels are not acceptable, then the above management strategies to enhance this population should be implemented. From a biological perspective we would recommend the harvest of male moose by licenced and nonlicenced hunters be reduced when the minimum adult sex ratio was reached. From a public relations perspective we recommend a complete closure of hunting prior to and during predator reductions. The level of predator reduction will depend on the number of moose desired and the time period in which to achieve that target. We recommend that both wolves and grizzly bears be reduced concurrently and that all age-sex bear classes be reduced in equal proportions. As in the previous strategy, harvest levels, when allowed, should be kept within sustained yield of the population and the minimum acceptable adult sex ratio. The population should be monitored prior to and after predator reductions. For further discussion on proposed management stategies for this population see "Recommendations Towards The Recovery of Moose and Caribou Population in the Whitehorse - Southern Lakes Area" (Yukon Fish and Wildlife Branch internal files, 1988).

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