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CAUSES AND RATE OF MOOSE MORTALITY IN THE SOUTHWEST YUKON

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Abstract: We examined the ways grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), black bears (*Ursus americanus*), and humans affected moose (*Alces alces*) numbers in a 6,310-km^2 area in the southwest Yukon during 1983–85. We documented pregnancy rates, birth rates, and causes and rates of natural mortality for female moose. Pregnancy, birth, and twinning rates were estimated as 84%, 114 calves:100 females, and 28%, respectively. The mean annual survival rate of adult females was 91%; most deaths occurred from May to October. Grizzly bears and wolves were the primary and secondary cause of adult moose mortality, respectively. Grizzly bears and wolves were responsible for 58 and 25% of all calf deaths, respectively, from known causes. Grizzly bears killed more moose calves then did wolves between birth and 20 June. After 20 June, wolves killed proportionately more calves than did grizzly bears. Grizzly bears, wolves, and licensed hunters accounted for 50, 26, and 9%, respectively, of all adult and calf mortalities over 1 year. We suggest that predation, primarily by grizzly bears followed by wolves, limited the growth of this moose population. This study demonstrates the relative significance of grizzly bear predation to other sources of moose mortality (natural and hunting) and the absolute significance of grizzly bear predation on a northern moose population. Moose calves should be radiocollared prior to 1 week of age to determine rates and causes of early neonatal mortality.

Moose are the most important big game species to subsistence and sport hunters in the Yukon. Approximately 10% of the resident harvest and hunting effort is concentrated in 1% of the land area in southwest Yukon. The nonconsumptive use of this resource is also focused in the southwest Yukon where, along with the Alaska Highway, 75% of the Yukon's human population occurs. Because of the intensive use of moose, a comprehensive understanding of the moose population status and the factors limiting population size was needed to effectively manage this resource. The population was considered

stable between 1981 and 1983 at a density of 190–250 moose/1,000 km^2 with low calf:female (18–30:100) and yearling:female (4–22:100) ratios (Larsen 1982; D. G. Larsen, unpubl. data). Neonatal calf mortality to 6 months of age was estimated to be between 80 and 86% in 1981 (Larsen 1982).

We suspected predation was 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 (Ballard and

Larsen 1987). Our study was designed to assess proximate causes of calf and adult female moose mortality using radio-marked animals from 1983 through 1985.

STUDY AREA

The 6,310-km² study area was located adjacent to the British Columbia–Yukon border. 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 >1,500 m, and large water bodies) (Larsen 1982). 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*) was prevalent. Paper birch (*Betula papyrifera*) and poplar (*Populus* spp.) were scattered throughout valley floors. Forest fires have been suppressed in this area for >2 decades. The 30 year mean annual temperature and precipitation at Whitehorse was −1.2 C and 261 mm, respectively. Snow accumulation averaged 67 cm. During our study, temperature, precipitation, and snow accumulation reflected the long-term average. The physiography, climate and vegetation of this area have been described (Oswald and Senyk 1972; D. Davies, C. E. Kenneday, and K. McKenna, Resource inventory southern lakes, Yukon Gov. Intern. Rep., Whitehorse, Yukon, 151pp., 1983).

Wolf, grizzly bear, and black bear were the major predators inhabiting the study area. Midwinter wolf densities in 1982 were approximately 12 wolves/1,000 km² of total land area (R. D. Hayes, Yukon Territ. Gov., unpubl. data). Wolf numbers were reduced from an estimated 74 animals in the fall of 1982 to 37 by late winter, prior to the beginning of the moose mortality study in 1983. The wolf population increased to 63 wolves in the fall of 1983, and was then reduced to 35 in March 1984. A population of 54 wolves in the fall of 1984 was reduced to 14 in March 1985. Reductions prior to 1983 likely did not affect moose survival rates, as the majority of wolves were removed around the northern and eastern periphery of the study area and the majority of the collared moose were in the central and western portions of the study area. Sixteen grizzly bears/1,000 km² of total land area were estimated in the study area in 1985 (D. G. Larsen, unpubl. data). One, 8, and 10 grizzly bears were harvested in 1983, 1984, and 1985, respectively. Black bears occur sporadically in forests and subalpine habitats. Densities were unknown, but thought to be similar to grizzly bear densities.

METHODS
Estimating Adult Female Parameters

We captured 39 and 5 female moose ≥22 months of age in March 1983 and 1984, respectively. Random search of all habitats by helicopter was made to locate and capture moose. Animals were captured as they were encountered. Moose were immobilized with carfentanil, xylazine hydrochloride, fentanyl citrate, and hyaluronidase (Larsen and Gauthier 1989).

Age was determined by tooth-cementum annuli from incisors (Sergeant and Pimlott 1959, Gasaway et al. 1978) of 43 females. Pregnancy was determined through rectal palpation (Arthur 1964, Haigh et al. 1982) of 43 moose during March–April of 1983 and 1984. Timing of birth and the number of calves born were determined through daily visual monitoring of radio-collared females during the 1983 and 1985 calving periods. Calves that were collared in 1983 and still alive in May 1985 were included in the adult mortality estimate in 1985 and 1986. Collars with 6-hour mortality switches were used (Telonics, Inc., Mesa, Ariz.), and all immobilized moose were monitored within 48 hours of administering the antagonist to identify capture-related deaths. Females accompanied by a

calf were monitored daily from mid-May through mid-July in 1983 and 1985, and weekly in 1984. Females were located 1–2 times a month during the remainder of 1983–84 and 1984–85. In 1985–86 females were monitored once in September, November, and April. Survival rates of adult females were estimated by dividing the number of females collared at time t and still alive at time $t + 1$ by the number of collared females at time t. Three intervals were used: 12-month annual period (17 May–16 May); 6-month snow-free period (17 May–1 Nov); and 6-month snow period (2 Nov–16 May). Only female moose monitored throughout an entire biological year were used in calculating survival rates. We determined the cause of mortality by evidence at the mortality site including predators seen, presence of bear or wolf hair, tracks or scats, presence of buried carcass, percent of the carcass hide present, presence of prey stomach contents, percent of the carcass found, and radius of the area over which the carcass was spread. Hair samples were distinguished based on color, texture, and medullar and cuticle scale patterns (Adjordan and Kolenosky 1969, Kennedy and Carbyn 1981). Scats were identified as bear or wolf based on size and shape characteristics. The percent hide and carcass remaining were visually estimated. The identity of predators was not determined for mortalities occurring between mid-July 1985 and May 1986 due to the infrequent level of monitoring, or at sites that were not investigated from the ground.

Estimating Calf Parameters

Two types of calf : female groups, based on collar status, were used in this study: collared calves with collared females ($n = 40$) and collared calves with uncollared females ($n = 79$). Sixty and 59 newborn calves were collared in 1983 and 1985, respectively. Calves were located from a helicopter during daily monitoring flights, physically restrained, and collared after the helicopter separated the calf from the female (Larsen and Gauthier 1989). We used expandable-breakaway collars (Schlegel 1976) on transmitters equipped with 2-hour mortality switches (Telonics, Inc., Mesa, Ariz.) for calves.

The ages of calves with collared females were determined from daily monitoring flights of the same females. The ages of calves with uncollared females were based on the following characteristics that were observed in calves of known age: 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; a 1-day-old calf was steady on its feet, or slowly walked towards the field crew, or attempted to follow the female; a 2-day-old calf walked quickly after the cow when approached by the field crew; and a 3–7 day-old calf ran after the female when approached but could still be caught by the field crew. Calves that were too mobile to be captured on the ground were judged to be >1 week old.

The causes of mortality were determined from collared calves during 1983 and 1985, and differences between years were tested by Chi-square analysis. All mortalities were investigated immediately upon receiving a mortality signal. When a mortality signal was detected, the helicopter descended to between 50 and 150 m above ground level and an area within approximately 1 km 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 as described for females. Although sign was recorded at each mortality site, the descriptive analysis of sign was limited to sites with evidence from a single predator species, and to grizzly bear and wolves. Sample sizes for minor causes were considered too small for meaningful analysis.

Causes of mortality were initially classified as: grizzly bear, wolf, black bear, grizzly bear or wolf, grizzly bear or black bear, predator unknown, and non-predator causes (e.g., drowning). The dual predator groups (responsible for 8 of 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 females with offspring (cubs of the yr, yearlings, or 2 yr olds) or adult bears of unknown sex. In 1985, bears found on carcasses were immobilized and classified according to sex and age (D. G. Larsen, unpubl. data).

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 a helicopter or fixed-wing aircraft 1–4 times/day from birth to the end of June, 1 time/week through July, 2 times/month to December and 1 time/month to May. In 1985, calves were monitored 1–4 times/day between birth and the

end of June, 1 time/day to July 15 and once in September, October, November, and March. If >1 week lapsed between calf relocations, cause of mortality was not assigned, with the exception of 7 cases 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 ($n = 39$) with uncollared females in 1983 and from collared calves ($n = 57$) with collared and uncollared females in 1985. Calves of collared females were excluded from the 1983 analysis due to the negative effects of immobilizing females on postnatal calf survivorship in this study area (Larsen and Gauthier 1989). This effect was only detected in the year the female was immobilized, therefore, calves of females immobilized in 1983 and 1984 were used to estimate calf survival rates in 1985.

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

A second measure of calf survival for calving and post-calving 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 mean (1983 and 1985) birth rate. Moose population size and composition were estimated for the study area following Gasaway et al. (1986*b*) and Larsen (1982).

The influence of birth period (early born 17–22 May, peak born 23–29 May, and late born 30 May–9 Jun), and female age (inexperienced 1–5 yr, experienced 6–9 yr, and old 10–15 yr) on calf survival was assessed by comparing the number of days between birth and death to birth period, and calf survivorship status (alive or dead) after 1 year to female age. Calf survivorship by sex was assessed by comparing calf status after 1 year to the sex of the calf.

Estimating Moose Population and Hunting Status

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 annually for May 1983 and May 1984. 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 mort. ities 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. These extrapolations assume the causes and rate of adult male and yearling natural mortality were equal to that measured for radio-collared adult females.

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; estimates were not available for non-licensed native hunters.

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

RESULTS

Productivity and Natural Mortality of Adult Females

Thirty-six (84%) of 43 females ≥24 months old were pregnant and the mean (1983–85) birth rate (calves born/pregnant and non-pregnant F, $n = 65$) was 114 calves:100 females. Twins were observed with 16 (28%) of the 58 collared females with calves. The mean age of females was 8 ± 0.05 (SE) years.

The causes and rate of adult female mortality were estimated for 33, 34, and 41 radio-collared females in 1983, 1984, and 1985, respectively. Ten (23%) of 43 collared females died from 1983 through 1985. Thirty percent died from unknown causes; known predators accounted for 60% and unknown predators 10% (Table 1).

The mean annual survival rate of females was 91% during the study (Table 2). Eight of the 10 mortalities occurred during the summer, yielding a mean snow-free survival rate of 93%. Only 2 collared females died during the winter. From wolf predation studies conducted in the same area (R. D. Hayes, unpubl. data) we estimated

Table 1. Causes and rates of annual (May–Apr) mortality of collared moose females, southwest Yukon Territory, 1983–85.

Mortality	1983–84	1984–85	1985–86	Combined
F present[a]	39	34	41	114
Lost contact	4	0	0	4
Capture related deaths	2	0	0	2
Remaining at end of period	33	34	41	108
Natural mortality:				
Grizzly bear	1	1	1	3
Wolf	2	0	0	2
Wolf and grizzly bear	1	0	0	1
Unknown predator	0	0	1	1
Unknown causes	0	1	2	3

[a] F were captured in 1983 (n = 39) and in 1984 (n = 5). Collared F present in 1984–85 were those surviving as of May 1984 and the 5 collared in March 1984. Collared F present in 1985–86 were those surviving as of May 1985 and the 9 1983 collared calves (now classified as ad) which survived to May 1985.

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 (R. D. Hayes, unpubl. data) this represents 54 adult female moose. The estimated female population (n = 598) in November 1983 was calculated for a comparable study area (D. G. Larsen, unpubl. data). Based on these results, approximately 9% of the female population was killed by wolves during the winter in 1983–84, as compared to 2% indicated by radio-collared females. We believe the true mortality rate was somewhere between 2–9%.

All 3 females killed by grizzly bears had calves and 1 of these was likely in labor. Two out of the 3 females killed by grizzly bears died during the calving period (14 May–5 Jun) and the third shortly after (25 Jun).

Extent and Causes of Calf Mortality

Calving occurred from 17 May to 10 June,

with a median calving date of 25 May; about 72% of calves were born over a 9-day (22–30 May) period (Fig. 1). No difference (P = 0.11) was found in the mean calving date between years. Calves were collared at a mean age of 2 ± 0.17 days.

Of the 119 calves used to determine causes of mortality, 1 died as a result of handling and contact was lost with another. Of the remaining 117, 95 died over 1 year. Eleven died from unknown causes. Of the 84 calves that died from known causes, predators accounted for 92% (77 of 84) and grizzly bears were the primary predator (Table 3).

No significant difference was found in the known causes of mortality between years (P = 0.32) or between calves with collared and uncollared females (P = 0.68). A higher proportion of unknown causes was recorded in 1985 because frequency of monitoring was reduced after July 1985 compared to 1983, so only known causes were used for comparisons between years and combined totals.

Of 77 calf mortality sites analyzed for predator sign, predators were observed at 39% of the sites. Grizzlies were seen at 20 of 45 kills attributed to grizzlies and wolves at 3 of 18 kills attributed to wolves. In all but 1 of the cases involving grizzlies, we observed the bear covering the carcass with dirt and vegetation, resting beside the carcass, or walking a short distance from the kill. The 1 exception was the observation of a female and 2 yearlings chasing and killing a calf.

Grizzly hair was found at 83% of kills attributed to grizzlies, and 29 and 64% of grizzly kill sites contained grizzly tracks and scats, respectively. In contrast, wolf hair was found at 94% of wolf kill sites, and 56 and 50% of wolf kill sites contained wolf tracks and scats, respectively. Calf carcasses were buried at 68 and 0% of the grizzly and wolf kill sites, respectively (G = 32.5, P < 0.01). Carcass stomach contents were absent at 85% of grizzly kill sites and 47% of wolf sites; a statistically significant difference

Table 2. Survival rates of collared female moose by time period in the southwest Yukon Territory, 1983–85.

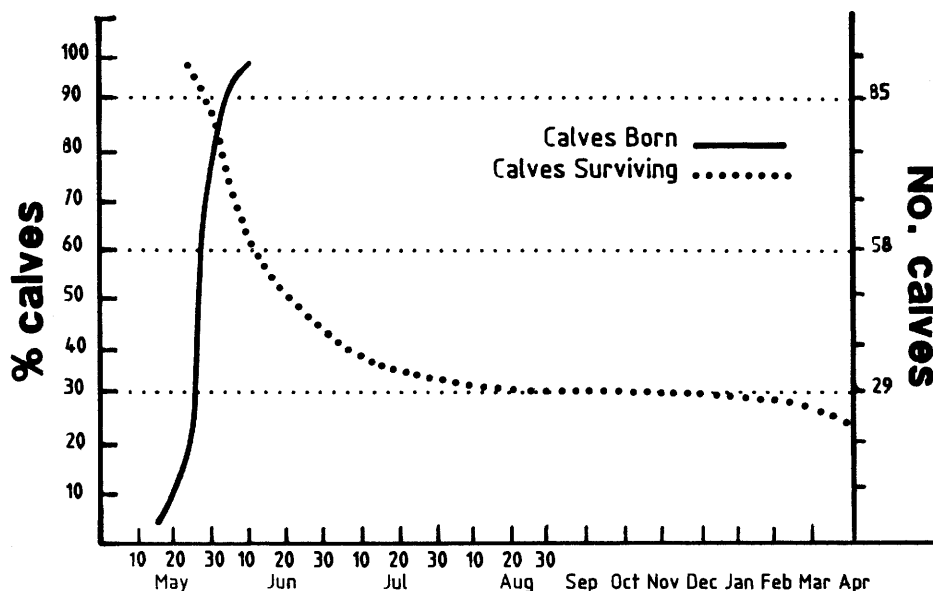| Period	1983		1984		1985		Combined	
	n	%	n	%	n	%	n	%
Summer (17 May–1 Nov)	33	88	34	94	41	95	108	93
Winter (2 Nov–16 May)	29	100	32	100	39	95	100	98
Annual (17 May–16 May)	33	88	34	94	41	90	108	91

Fig. 1.   Timing of birth and death of radio-collared moose calves southwest Yukon Territories from 1983 to 1985.

($G = 9.3$, $P < 0.01$). Ninety percent or more of the calf hide was present at 46% of grizzly kill sites, but at only 6% of wolf sites. Grizzly bears tended to "skin" a moose calf carcass leaving much of the hide intact, in contrast to wolves that tore or shredded hides from the carcass. Calf hides at grizzly kill sites were often inverted. The lack of hide ingested by grizzly would result in the absence of hair in bear scat. This was the case with bear scats observed at kill sites. Typically, a pile of bones, the hide, and the radio collar were found at the burial site. The ribs, scapula, lower jaw bones, cranial bones, leg bones, and detached hoof sheaths were often found. Several scat piles and beds were often found and a musky odor was present.

Unlike grizzlies, wolves scattered the carcass over a wide area (>300 m from the kill site) and tended to crush all bones, except for the heavier parts of the leg bones and mandibles.

Several small bone piles or individual bones were found in the general area. The radio collar of the dead calf was often found 50–100 m from the nearest predator evidence. The mean radius of carcass spread by wolves (122.2 m) was significantly greater ($P < 0.01$) than by grizzlies (18.2 m).

Between birth and 20 June, grizzly bears and wolves accounted for 60 and 10%, respectively, of the calves that died. After 20 June, wolves accounted for 54 and grizzlies 27% of the calves that died. The latest a collared calf was killed by a grizzly bear was 4 August.

In 1983 and 1985, 12 bears or bear groups were observed feeding on calves. Seven of the 12 bears were females with offspring (2 with cubs of the yr, 5 with yearlings or 2 yr olds), 3 were males (2–7 yr olds and 1–2 yr old) and the sex and age of the remaining 2 were unknown.

We estimate 250 calves killed by grizzlies in 1983 (Table 4). At a density of 16 bears/1,000 km², with adults (≥6 yr) representing 49% of the population (D. G. Larsen, unpubl. data), approximately 49 adult bears would prey on 250 calves for a mean annual kill rate of 5.1 calves/ adult bear.

Most calf mortalities in 1983 and 1985 combined occurred within 8 weeks of birth (Fig. 1). Of the 96 radio-collared calves used in this analysis, 44 (46%) died by 20 June, 65 (68%) by 1

Table 3.   Causes of annual (May–May) mortality of 119 collared moose calves, southwest Yukon Territory, 1983 and 1985.

Mortality	1983 n	1983 %	1985 n	1985 %	Combined n	Combined %
Grizzly bear	34	62	15	50	49	58
Wolf	14	26	7	23	21	25
Black bear	1	2	3	10	4	5
Unknown predator	2	4	1	3	3	4
Non-predator (natural)	3	6	4	13	7	8

Table 4. Total annual moose mortality and the relative importance among causes, southwest Yukon Territory, May 1983–May 1984.

Causes of mortality	Calves	Ad and year-lings	Combined n	Combined %
Grizzly bear	250	19	269	50
Wolf	103	37	140	26
Black bear	7	0	7	1
Grizzly/wolf	0	19	19	4
Unknown predator	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 yearlings at calving in 1984 ($n = 74$) from the estimated number of calves born in 1983 ($n = 486$) (Table 6). This total was then divided among the various causes of mortality recorded in 1983 (Table 3).

[b] Total ad and yearling deaths were determined by subtracting the estimated number of ad at calving in 1984 ($n = 540$) from the estimated number of ad and yearlings at calving in 1983 ($n = 661$) (Table 6). This total (-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.

November and 72 (75%) died by 1 year of age (Table 5). Of the 72 calves that died during their first year, 23 (32%) died before they were 10 days old, 59 (82%) died by 15 July and 65 (90%) by 1 November.

The relative time period of birth may affect calf survival; i.e., late born calves would have a better chance of surviving if predators were saturated by the number of calves available during the early and peak born periods, or the primary predator (grizzly bear) switched from meat to vegetation over the calving period. However, no significant differences ($P = 0.33$) were found between the birth period of the calf and the number of days that it survived.

Calves depend on their mothers for protection. If adult moose vulnerability to wolf predation increases with age (Peterson 1977, Peterson et al. 1984) it is possible that older females are less able to defend their calves from wolves and grizzly bears compared to younger females. However, no difference ($P > 0.05$) was found in the proportion of dead to live calves in relation to the age class of the female.

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 the above potential biases, the effects of collaring the calf on its survival were tested and found to be negligible (Larsen and Gauthier 1989).

Relative Causes of Adult and Calf Mortality

We determined the relative and absolute significance among the natural causes of moose mortality and hunting (Table 4). We estimated that between the 1983 and 1984 calving periods 534 deaths occurred (412 calves and 75 ad and yearlings died from natural causes, and 47 ad and yearlings were killed by hunters). Of the 534 total mortalities, grizzly bears, wolves and hunting accounted for 50, 26, and 9% of all deaths, respectively (Table 4). Because winter predation on adult females may have been underestimated, wolves may account for a higher percentage of the total annual moose mortality than shown in Table 4. Overall losses of adults to wolf predation, however, would not exceed losses of calves to grizzly predation. We conclude that predation by grizzly bears was the dominant proximate cause of all major sources of moose mortality and the major factor limiting moose population growth during the study period.

Estimated calf survival rates to 1 November (23%) from radio-collared calves in 1983 (Table 5) was identical to survival rates generated from the model over the same time period (Table 6). This agreement in 2 independent estimates of calf survival suggests that the rates presented reflect the actual survival rate.

DISCUSSION

Productivity and Natural Mortality of Adult Females

Grizzly bears were the primary known natural cause of adult female mortality during this study. Ballard et al. (1988), Boertje et al. (1988) and Gasaway et al. (1986a) also have reported significant levels of grizzly bear predation on adult moose in Alaska.

Our finding that most adult female mortalities occurred during the period when bears are active (May–Nov) supports the conclusion that grizzly bears were the primary cause of female mortality. In contrast Peterson (1977) and Peterson et al. (1984) reported the majority of predation on adult moose occurred during winter and early spring on Isle Royale, Michigan, and Kenai Peninsula, Alaska, respectively. Grizzly bears were absent or scarce in the areas.

All predation by grizzly bears on females occurred in the calving–post-calving period. Boertje et al. (1988) concluded that grizzly bear

Table 5. Survival rates of 96 collared moose calves, southwest Yukon Territory, 1983 and 1985.

Period	1983		1985		Combined	
	n	%	n	%	n	%
Calving (17 May–20 Jun)	39	41	57	63	96	54
Post-calving/summer (21 Jun–1 Nov)	16	56	36	61	52	60
Winter (2 Nov–16 May)	9	67	22	82	31	77
Annual (16 May–17 May)	39	15	57	32	96	25

predation rates on adult moose were highest during the spring. Pregnant females may be vulnerable to predation during calving because they are less mobile than nonparous females and because they defend newborn calves.

Extent and Causes of Calf Mortality

We contend that predators observed at or near moose calf mortality sites were the causes of mortality and were not simply scavengers. We monitored moose calves up to 4 times/day and calves were located no later than 12 hours from the time of death in 67 of 77 cases. Work in south-central Alaska (Ballard et al. 1981), where predator–prey densities were similar to those in this study, suggests that large carnivores do not find moose calf carcasses until ≥30 hours after death. A comparable study on the Kenai Peninsula (Franzmann et al. 1980) found that calves were not scavenged by wolves and bears within 1 day of death, nor were calves that were checked 8–10 days after death scavenged by wolves or bears. Ballard et al. (1988) found that grizzlies remained on calf moose kills for an average of 13 hours. And finally, Boertje et al. (1988) concluded that radio-collared grizzlies in southeastern Alaska kill 4× more animal biomass than they scavenge.

We documented a shift from grizzly bears to wolves as the major source of mortality for moose calves after mid-June. This shift may have been the result of decreased vulnerability to bear predation due to increased mobility of calves (Ballard et al. 1980), decreased availability of calves after mid-June, or decreased availability of the vegetative food source for grizzly bears. Other studies have also shown that grizzly bear predation on moose calves is highest during the first month after birth (Ballard et al. 1981, 1988; Boertje et al. 1987, 1988).

The pattern of calf mortality in this study is comparable to other areas where bears were abundant. Gasaway et al. (1986a) reported that

in east-central Alaska, predators accounted for 23 of 27 (85%) calf deaths over 1 year, and that grizzly bears were responsible for 17 of 27 mortalities. Franzmann et al. (1980) reported that black bears killed 34 of 53 calves prior to late summer on the Kenai Peninsula, Alaska. Ballard et al. (1981) estimated that grizzly bears killed 52 of 63 calves prior to November in the Nelchina Basin, Alaska.

Our data suggest 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 or that the other predators spent more effort on other prey. During the 1983 and 1985 calf mortality studies, grizzly and black bears were thought to occur at similar densities, yet grizzly bears accounted for 12× the number of deaths. Ballard et al.

Table 6. Moose population size and composition between May 1983 and May 1984, southwest Yukon Territory.

Estimated composition	Estimated calving population 1983[a]	Estimated post-hunt fall population 1983[b]	Estimated calving population 1984[c]
Ad M	215	153	161
Ad F	426	371	379
Yearling M and F	20	16	74
Calf	486	111	432
N	1,147	651 ± 143[d]	1,046

[a] Ad and yearling population estimates at calving 1983 were determined by applying the 1983 May–Nov natural survival rate (88%) documented for ad F to the ad and yearling cohorts (Table 2). Hunting losses occurred between Aug–Nov 1983 and comprised 41 ad M, 2 yearling M, and 4 ad F. These are minimum values as the unlicensed 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 F present at calving by the documented birth rate (114 calves : 100 F).

[b] Estimated from an aerial survey conducted in Nov 1983 (D. G. Larsen, unpubl. data).

[c] Calving 1984 population estimate was calculated from the overwinter survival rates of 67% for calves and 100% for ad and yearlings. Fall 1983 yearlings which survived to calving 1984 were assumed to have an equal sex ratio and were divided equally between the ad M and F groups.

[d] 90% CI.

(1988) concluded, 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× the number of calf deaths to November. The results from these 2 studies suggest that grizzly bears are able to take more neonatal moose than black bears and wolves in some northern multi-predator systems.

Our results, as those of Ballard et al. (1988) and Boertje et al. (1988), suggest that most bears regardless of age, sex, and family status killed moose calves. Both studies reported considerable variability in predation rates by individual bears. The mean kill rate of 5.1 calves/adult bear in our study is similar to that reported from Alaska. Boertje et al. (1988) reported 5.4 calves/adult bear (F ≥5 yr and M ≥9 yr) for east-central Alaska and Ballard et al. (1988) reported 5.3 calves/bear (≥3 yr) for south-central Alaska. These consistent results suggest similarities in grizzly bear predation rates on moose calves over a wide geographical area. Boertje et al. (1988) concluded that predation by grizzly bears on moose calves is independent of moose density, based on studies in Alaska.

The survival curve for radio-collared calves is similar in shape to that reported for other moose populations subject to heavy predation. Franzmann et al. (1980) and Gasaway et al. (1986a) documented 57 and 76% mortality of radio-collared calves within 10 and 8 weeks of birth, respectively. Ballard et al. (1981, 1988) reported an 84% mortality rate to mid-July and a 55 and 82% mortality rate to 1 November, respectively.

Our 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 and causes of moose mortality in North America (Franzmann et al. 1980; Ballard et al. 1981, 1984, 1988; Stewart et al. 1985; Gasaway et al. 1986a; Ballard and Larsen 1987) and studies on grizzly bear predation rates (Ballard et al. 1981, 1988; Boertje et al. 1988) have 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 even in areas where they occur at low densities.

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SURVIVAL RATES OF ADULT FEMALE MOOSE ON THE KENAI PENINSULA, ALASKA

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Abstract: We determined survival and cause-specific mortality rates for 51 radio-collared adult female moose (Alces alces) on Kenai National Wildlife Refuge (KNWR), Alaska from 1980 to 1986. The mean annual survival rate was 0.92; collision with a vehicle was the primary cause of death (0.04/yr). Other mortality factors were natural accidents (0.01), old age (0.01), brown bear (Ursus arctos) predation (0.01), and hunting (0.01). Moose wearing non-functional collars died from poaching, vehicle collisions, starvation, and unknown causes. Collared moose were not killed by wolves (Canis lupus) although wolves were common. Survival rates were unaffected by area, year, or season and only decreased slightly as moose aged. Human-caused mortality was associated with roads, occurred at nearly twice the rate reported to authorities, and appeared non-selective to moose age or condition. Adult female moose survival was enhanced by restricted harvest and wolf control and was not limiting growth of the moose population on the Kenai lowlands.

Adult survival rate is an important factor influencing the population dynamics of long-lived species (Nelson and Peek 1982). Annual survival rates for adult moose range from 0.75 to 0.94 (Peterson 1977, Hauge and Keith 1981, Mytton and Keith 1981, Gasaway et al. 1983). The survival rates of moose 1–5 years old were often near 1.0 whereas rates for moose ≥11 years old were <0.60 (Mech 1970, Peterson 1977, Gasaway 1983). Habitat quality, winter severity, predator populations, hunting or poaching pressure, and parasites also influence moose survival rates (Coady 1982).

Densities of moose on the Kenai Peninsula were among the highest in North America (LeResche et al. 1974). Summer calf and adult

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