MOOSE MORTALITY IN EASTERN INTERIOR ALASKA

MARK R. BERTRAM,[1] U.S. Fish and Wildlife Service, Yukon Flats National Wildlife Refuge, 101 Twelfth Avenue, Fairbanks, AK 99701, USA

MICHAEL T. VIVION,[2] U.S. Fish and Wildlife Service, Yukon Flats National Wildlife Refuge, 101 Twelfth Avenue, Fairbanks, AK 99701, USA

Abstract: We investigated causes of mortality and the physical condition of moose (*Alces alces gigas*) in a multiple-predator system in eastern interior Alaska, USA, from 1998 to 2000. We identified the sources of mortality of calf and cow moose and collected fecundity and fitness data to obtain information on range quality and carrying capacity. Radiocollars were placed on 30 cow moose in 1998 and on 62 moose calves in 1998 ($n = 29$) and 1999 ($n = 33$). Estimates of fecundity and fitness parameters indicated that reproductive potential for moose was high, with a twinning rate of 63%, a pregnancy rate of 89%, and above-average body sizes of female and neonate moose. We inferred that range quality may not be a significant limiting factor for this population. We documented low neonate survival through the first 14 weeks of life (28%). Predation was responsible for 92% of known calf mortality; black bears (*Ursus americanus*; 45%) and grizzly bears (*Ursus arctos*; 39%) were the major causes of mortality. Despite low population densities in this region, grizzly bears were an important predator on neonates as well as adult female moose. Mean annual calf and adult female moose survival (20% and 88%, respectively) were similar to rates reported in other low-density moose populations in North America. We also estimated from 7 to 12% of the population was harvested annually by humans, and of that, illegal cow harvest constituted at least 33%. Our data suggest that low calf survival, adult mortality from wolf (*Canis lupus*) and grizzly bear predation, illegal cow harvest, and low predator harvest, all act in concert to maintain this moose population at a low density.

Estimating the vital statistics of an ungulate population is essential to understanding the mechanisms controlling its growth. Caughley (1977) maintained that to understand the dynamics of a population, one needs to know how many animals it contains and its rates of growth, production of newborns, and mortality. Recent work (Gaillard et al. 2000) suggests that an examination of fitness components (i.e., weight, size) also is necessary when examining population growth rates in large ungulates. Of these population parameters, it is especially difficult to assess specific causes and rates of mortality of neonates and adults due to the high cost of intensive monitoring. Acquiring this information on ungulate populations in northern latitudes can be further confounded due to their remote range and problems of scale. Despite these difficulties, a number of studies have examined causes and rates of mortality of neonate and adult moose (Franzmann et al. 1980; Ballard et al. 1981, 1990, 1991; Larsen et al. 1989; Osborne et al. 1991); however, only a few studies have collected detailed fitness data (Keech et al. 1998, 2000; Testa and Adams 1998).

We investigated causes of mortality and the physical condition of moose in a multiple-predator system in eastern interior Alaska. Although moose densities in this region historically have been low and appear to be suppressed, there has been little work to quantify factors that may be limiting population growth. Although human harvest of moose in the region is high, predator populations are lightly harvested. We use the phrase "lightly harvested" to describe bear or wolf populations where harvests cause a slight reduction in a predator population relative to their respective carrying capacity (K). Since moose generally is the only available ungulate prey in the region, there is a high proportion of predators to prey. To test what influence predators may be exerting on moose population growth, we designed our study to closely examine proximate causes of neonate and adult female moose mortality. We also collected fecundity and fitness data to give us insight into range quality and K.

STUDY AREA

The 16,835-km² study area is located on the western Yukon Flats in the northern boreal forest of eastern interior Alaska (Fig. 1). The study area is encompassed by the Yukon Flats National Wildlife Refuge and included in the western half of Game

[1] E-mail: mark_bertram@fws.gov

[2] E-mail: michael_vivion@fws.gov

Capture Areas

Calves

Cows

River

Beaver Village
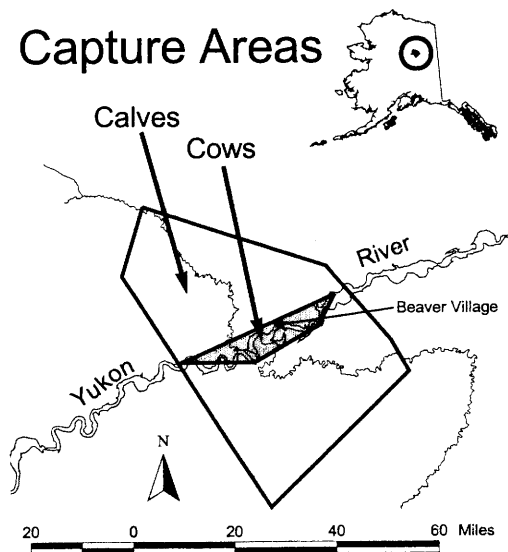
Yukon

N

20   0   20   40   60 Miles

Fig. 1. The study area in eastern interior Alaska, USA, showing capture locations of adult female and neonate moose, 1998–1999.

Management Unit 25D. It is situated near the village of Beaver, Alaska (66°21′N, 147°23′W). The Yukon Flats is a vast wetland basin bisected by the Yukon River. The basin is underlain by discontinuous permafrost and includes a complex network of lakes, streams, and rivers. The landscape is heavily influenced by flooding and wildland fire. The southern edge of the study area includes uplands and foothills near the White Mountains, with elevations ranging from 91 to 912 m.

The area is characterized by mixed forests, dominated by white spruce (*Picea glauca*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Shrub communities of alder (*Alnus*) and willow (*Salix* spp.) are most common in riparian sites and surrounding lakes and meadows. Dwarf shrubs such as glandular birch (*Betula glandulosa*), Labrador tea (*Ledum decumbens*), crowberry (*Empetrum nigrum*), and blueberry (*Vaccinium uliginosum*) are common in the uplands.

The Yukon Flats has a continental subarctic climate characterized by great seasonal extremes of temperature and daylight. Summer temperatures can exceed 38 °C and are warmer than any other comparable latitude in North America (U.S. Department of the Interior 1987). Winter temperatures may reach extremes of –59 °C or below. Although the area has a short growing season of

about 81 days, the long hours of sunlight during the spring and summer months produce lush vegetation. Annual precipitation is low, ranging from 18 to 28 cm. Snow accumulations rarely exceed 76 cm. Unlike other locations in interior Alaska, snow accumulation usually does not restrict movement of moose in winter.

Moose densities within the study area are between 120 to 180 moose per 1,000 km² (M. Bertram and M. Vivion, unpublished data). This density is similar to those reported in eastern Alaska (Gardner 1996), interior Alaska (O. Huntington, U.S. Fish and Wildlife Service, unpublished data), and the Yukon (Stenhouse et al. 1995). Based on high black bear capture rates (M. Bertram, U.S. Fish and Wildlife Service, unpublished data) and low hunting pressure adjacent to the study area, we suspect that black bear densities are between the range of densities previously reported in Alaska (86 to 265 per 1,000 km²; Hechtel 1991, Schwartz and Franzmann 1991, Miller 1994). Grizzly bear densities are suspected to be approximately 10 per 1,000 km², which is in the low range of densities reported by Miller et al. (1997) for Alaska. Wolf densities are estimated at 4 per 1,000 km² (R. Stephenson, Alaska Department of Fish and Game, unpublished data).

METHODS

We estimated moose densities in the study area using stratified random aerial survey methods described by Gasaway et al. (1986) and Ver Hoef (2001). Annual moose harvest data were taken from harvest surveys conducted by a local tribal government on the Yukon Flats (D. Schwalenberg, Natural Resources Department [Stevens Village, Alaska, USA], unpublished data).

Adult and Calf Capture

Thirty adult cow moose were darted and immobilized from a Bell Jet Ranger (206BIII) helicopter in March 1998. Moose were sedated with a mixture of 1.3 ml (4.0 mg/ml) carfentanil citrate (Wildnil®; Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) and 1.5 ml (150 mg/ml) xylazine hydrochloride (TranquiVed®; VEDCO, St. Joseph, Missouri, USA) administered from a Palmer Capchur® dart (Douglasville, Georgia, USA; Taylor 2001). The antagonist was 8 ml (400 mg/ml; 3 ml intravenous and 5 ml intramuscular) naltrexone hydrochloride (Trexonil®; Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) and 4 ml (400 mg/ml intravenous) tolazoline hydrochloride (Tolazine®; Lloyd Laboratories, Shenandoah,

Iowa, USA). Drug reversal times were recorded. Rectal temperature was monitored continuously while moose were immobilized.

Standard morphometric measurements recorded included total body length, chest girth, and hind foot length. Body length was measured from the hairless patch on the nose along the body contour to the tip of the tailbone. Chest girth was determined by doubling the distance from the sternum to the top of the hump. Teeth were visually examined for wear (Hindelang and Peterson 1994). Model 600 radiotransmitters (Telonics, Mesa, Arizona, USA), with a motion-sensitive mortality switch on 10-hour delay, were fitted to each cow moose. Approximately 20 to 30 ml of blood was drawn from the jugular vein for pregnancy-specific protein B assays and tested for presence of infectious bovine rhinotracheitis virus, bovine viral diarrhea virus, parainfluenza 3 virus, respiratory syncytial virus, epizootic hemorrhagic disease virus, bluetongue virus, and 5 serovars of *Leptospira interrogans*. An ear tag was fixed to the right ear of each moose; the tissue from the punch hole in the ear was retained for DNA testing. Body condition was rated on a scale of 1 to 10 based on the presence or absence of fat and muscle on the mid-torso, shoulder, ribs, and lower back (Franzmann 1977). Generally, moose classified as 8 and above are well fleshed, 7 is average, 4 to 6 below average, and 1 to 3 indicates malnutrition. Rump fat was measured using an Aloka model 500 ultrasound device (Aloka, Wallingford, Connecticut, USA) with a 5-MHz 8-cm linear-array transducer (Stephenson et al. 1999). Fat thickness was measured ultrasonically along the spine at the closest point to the upper femur. Subcutaneous fat along the spine line was also measured with electronic calipers. Personnel from the Moose Research Center (Soldotna, Alaska, USA) analyzed all rump fat and blood data. Cow moose were monitored using standard aerial radiotelemetry techniques biweekly from March through mid-May in both years.

Calf capture operations were initiated on 17 May 1998 and 20 May 1999. Adult cows were located daily by fixed-wing aircraft to determine the presence or absence of calves. A Bell Jet Ranger (206 BIII) was used to separate cows from neonatal calves and a 2-person team captured calves and fitted them with an expandable breakaway collar. Collars were custom made (Osborne et al. 1991) with 4 layers of PEG® elastic bandage wrap (Franklin Lakes, New Jersey, USA) and included a pocket for an 85-g radiotransmitter (Model 300; Telonics,

Mesa, Arizona, USA). Each transmitter included a 2-hour delay motion sensor. Calves were sexed, then weighed with a 35-kg Pesola scale. Teams wore rubber gloves and used individual burlap bags to weigh calves and to reduce human scent on the animals. In the case of twins, both young were captured, collared, and released simultaneously.

Calving Dates, Pregnancy Rates, Birth Mass, Incidence of Twinning, Mortality

Cows were located daily by fixed-wing aircraft from mid-May to mid-June to determine the presence of calves. Calves were classified as less than 1 day old if their dam had been observed without a calf the previous day. Additionally, the posture, coordination, and the condition of the umbilicus (i.e., bloody, wet, dry, or absent) was noted for each calf during capture to assess age (Adams et al. 1995). Birth mass was estimated for calves >1 day old at the time of capture by subtracting 0.6 kg for each day >1 (Keech et al. 2000). Only calves of known age were included in the sample to determine mean birth weights. Twinning rate calculations included both collared cows and uncollared cows with 1 or 2 calves <2 days old at first observation. Locations of uncollared cows with young were recorded daily to prevent double counting and visual cues were used to determine if calves were <2 days old (i.e., wet appearance, wobbly, or unable to walk).

Collared cows and calves were monitored by daily radiotracking flights with fixed-wing aircraft through the end of June, a minimum of 2 times each week during July, and once each week for the next 90 days. A helicopter was used to access kill sites immediately after detecting a mortality signal. Kill sites were initially examined from aircraft to search for predators. Methods described by Ballard et al. (1979) were used to determine causes of mortality. At each site, hair and scat samples were collected, tracks were inspected, carcasses were examined for puncture marks and wounding patterns, and photographs were taken. Hair samples were sent to the University of Idaho for DNA analysis to determine predator species (Shields and Kocher 1991, Waits 1996) and gender (Taberlet et al. 1993, Woods et al. 1999), and to identify individual markers (Paetkau et al. 1995). Uncollared calves were presumed dead if they were not observed with a collared cow on 2 consecutive relocation flights.

Statistical Analyses

Proportions were compared with the *Z*-test to analyze between year variation in pregnancy
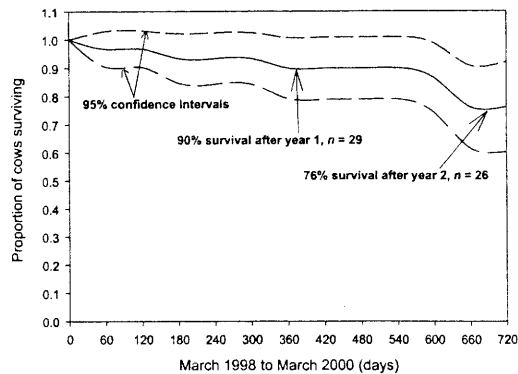
Fig. 2. Survival estimates for cow moose in eastern interior Alaska, USA, 1998–2000, using Kaplan-Meier method with staggered entry design.

rates, incidence of twinning, survival rates, and intra- and inter-year variation of mortality sources (Freund and Wilson 1997:200). Two-tailed *t*-tests using pooled variances were used to test for differences in birth mass between litter sizes, sexes, and years (Zar 1984:126). We tested for differences in median dates of birth using the 2-sample median test (Zar 1984:145). Moose survivorship was determined using the Kaplan-Meier method with staggered entry design (Pollock et al. 1989). The Kaplan-Meier method was flexible in that it allowed for censorship of animals removed from the population due to radio failure, collar loss, or emigration, and it allowed for new animals to be added after initiating the study. All groups were assumed to be independent for all analyses.

RESULTS

Harvest data indicate 40 bulls and 20 cows are harvested annually from the study area (D. Schwalenberg, Natural Resources Department [Stevens Village, Alaska, USA], unpublished data). The moose population estimate in 2000 for the study area was 87 to 141 moose per 1,000 km^2 (M. Bertram, unpublished data).

Adult Measurements, Back Fat Depths, Mortality

Thirty cow moose were captured and fitted with radiocollars between 16 to 18 March 1998 (Fig. 1). Ten of these cows were accompanied by calves at the time of capture, including 2 sets of twins.

Based on examination of tooth-wear patterns, all cow moose likely ranged from young to prime age adults (i.e., <10 years). Body conditions of cows ranged from 5.5 to 8. The mean and median con-

dition index values were 7.1 and 7.0, respectively. Nine moose were rated 8, indicating that noticeable fat was present. Ultrasound tests indicated that median rump fat thickness was 1.0 cm (range 0 to 1.8 cm, SD = 0.7, *n* = 13), and median ingesta-free body fat was 7.8% (Stephenson et al. 1999).

Blood analyses indicated little evidence of exposure to disease agents; however, 1 animal (M-27) had a very low level of antibody to 1 of the serovars of *Leptospira interrogans*. The specific serovar, known as *canicola*, can cause chronic kidney disease (R. L. Zarnke, Alaska Department of Fish and Game, personal communication).

The survival rate for collared cows (*n* = 29) in year 1 (16 Mar 1998–15 Mar 1999) and year 2 (*n* = 26, 16 Mar 1999–15 Mar 2000) was 90% and 85%, respectively. No significant difference occurred in survival rates between years (*P* > 0.3). Total survivorship for cow moose through year 2 was 76% (Fig. 2). Two cows were killed by grizzly bears, 1 in early April 1998, the other in September 1998. Four cows were killed by wolves in February 2000 in or near the Yukon River. Two cows shed collars, 1 in October 1998, and the other in late December 1999. One cow was harvested illegally in March 1999.

Calving Dates and Site Fidelity, Pregnancy Rates, Incidence of Twinning

Calving dates in both years (*n* = 51) ranged from 14 May to 9 June with a median calving date of 24 May. In 1998, calving dates (*n* = 23) ranged from 18 May to 5 June with a median date of 25 May; the mode was 24 May (*n* = 5). Calving dates in 1999 (*n* = 28) ranged from 14 May to 9 June with a median date of 23 May; the mode was 18 May (*n* = 5). Two-sample median tests indicated no significant differences between years (*P* > 0.7).

Site fidelity of dams to birthing locations between years was low. The distances between calving sites for 26 cows ranged from 0.3 to 55.9 km with a mean of 9.2 km. Only 5 of 26 dams birthed less than 1 km from the location of the previous year.

We observed calves with 49 of 55 collared cows for an observed mean pregnancy rate of 89% (Table 1). Although a comparison of pregnancy rates between years indicated a significant difference (*P* = 0.007), we suspect that the actual pregnancy rate in 1998 may have been 100% based on the results of pregnancy-specific protein B analyses (Table 1). We observed 38 cows with twins and 22 cows with singletons during the 2-year period, for a twinning rate of 63%. No significant differ-

Table 1. Observed and estimated pregnancy and twinning rates for moose cows monitored in eastern interior Alaska, USA, 1998–1999.

Parameter	1998			1999			All years		
	n	Observed	Estimated	n	Observed	Estimated	n	Observed	Estimated
Pregnancy rate[a]	29	0.79	1.00	26	1.00	n/a	55	0.89	n/a
Twinning rate[b]	27	0.66	0.70	33	0.61	n/a	60	0.63	n/a

[a] Pregnancy estimates derived from pregnancy-specific protein B analysis (Alaska Moose Research Center, Soldotna, USA). Conducted only in 1998.
[b] Calves more than 2 days old were not used in twinning estimates.

ence occurred in twinning rates between years ($P > 0.3$).

Calf Mass

Only calves of known age were included in our analysis of mass ($n = 41$). Mean adjusted birth mass was 19.1 kg (range 15 to 25 kg, SD = 1.7, $n = 11$) for singletons and 16.8 kg (range 12 to 21.8 kg, SD = 1.2, $n = 30$) for twins. Birth mass for singletons and twins was significantly different in 1999 ($t = 2.35$, df = 24, $P = 0.03$) and between years ($t = 2.38$, df = 39, $P = 0.02$). Birth mass ($P > 0.5$) was similar for males (mean 17.2 kg, range 14 to 24.4 kg, SD = 1.4, $n = 22$) and females ($\bar{x} = 17.7$ kg, range 12 to 25 kg, SD = 1.5, $n = 19$).

Calf Mortality, Survival Rates

We captured and radiocollared 62 calves during 2 calving seasons (17 May–7 June 1998, $n = 29$ and 1999, $n = 33$; Fig. 1). Four calves died from trampling by the dam or abandonment; these capture-induced mortalities were removed from the sample for survival analysis. We observed 2 stillbirths, 1 each in 1998 and 1999; each was associated with a live calf.

We examined 39 calf carcasses and attributed 36 of these mortalities to predators (Table 2). Black bears accounted for 17 of 38 (45%), and grizzly bears accounted for 15 of 38 (39%) mortalities. The incidence of black bear and grizzly bear mortality did not differ between years ($P > 0.3$). We found 3 calves that had drowned under circumstances suggesting they had retreated to the water to escape from bears. Two had drowned in a lake filled with woody debris, and black bears were present on both sides of the lake. Another drowned in a creek apparently because it was unable to climb a steep cutbank; its sibling was killed nearby by a grizzly bear. One calf was killed by wolves, and 2 were killed by unknown predators. One calf died of undetermined causes. We were unable to visit 25 sites where calves died. Eighteen of these mor-

talities included uncollared calves. The remaining 7 involved collared calves that died in inaccessible locations or whose collars malfunctioned.

We observed bears at 14% of calf mortality sites investigated for predator sign. Black bears and grizzly bears were seen at 2 sites each. Bear hairs, scats, and tracks were observed at 88%, 29%, and 6%, respectively, of kills attributed to black bears and at 93%, 60%, and 40%, respectively, of kills attributed to grizzly bears.

Generally, calf remains found at most bear kill sites included small pieces of leg and cranium bones, the hooves, and the radiocollar—all of which were usually found within several meters of each other. Similar to Larsen et al. (1989), calf hides were inverted at grizzly kill sites, and carcasses usually were partially buried with soil. Freshly buried carcasses were mostly intact, but in most cases the cranium was broken and the brain was removed. The presence of hooves and small leg and cranial bones, and the absence of the hide and digging typified black bear kill sites. At fresh black bear kill sites (less than 2 hr old) 1 or more legs were removed, the cranium was crushed with the brain removed, and in 2 cases the tongue had been removed. We documented

Table 2. Fate of moose calves monitored from birth to 1 year old (May to May) in eastern interior Alaska, USA, 1998–1999.

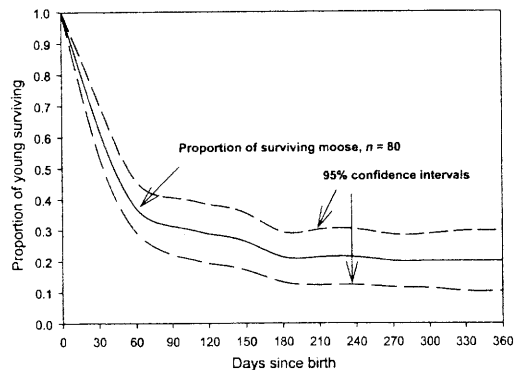| Parameter	1998		1999		All years	
	n	%	n	%	n	%
Censored calves	0	0	3	8	3	3
Causes of mortality						
Black bear	9	23	8	20	17	21
Grizzly bear	8	21	7	17	15	19
Wolf	0	0	1	2	1	1
Unknown predator	1	3	1	2	2	3
Drowning	3	8	0	0	3	4
Unknown cause	12	30	14	34	26	33
Surviving calves	6	15	7	17	13	16
Total	39	100	41	100	80	100

Fig. 3. Survival estimates for calf moose in eastern interior Alaska, USA, 1998–2000, using Kaplan-Meier method with staggered entry design.

only 1 calf killed by wolves, and in that instance, the bones were widely scattered.

Of the 33 predator hair samples examined for species, sex, and individual DNA markers, 19 black bears and 7 grizzly bears were identified. The remaining 7 contained 1 mixed sample (both species) and 6 failed extractions. The 6 failed extractions did not amplify the bear's specific identification primers. Of the 26 bears identified to species, 19 were identified as different individuals (16 black, 3 grizzly), including 18 males (15 black bear, 3 grizzly) and 1 female (black bear).

Annual survival rates were calculated for the periods of 20 May 1998–19 May 1999 and 20 May 1999–19 May 2000. Three calves were censored from the second year's sample due to the uncertainty of their death. In all 3 cases, the dam was killed by wolves and the fate of the calf was unknown. Annual survival rates for collared calves in 1998 and 1999 were 17% and 24%,

respectively, with a mean rate of 21% (n = 58; Fig. 3; Table 4). We also monitored 16 collared cows with 22 uncollared calves during the 2-year period. Uncollared calves had annual survival rates of 10% in 1998 and 25% in 1999, and a mean rate of 18% (n = 22). Annual survival rates in 1998 and 1999 for all monitored calves were 15% and 24%, respectively, with a mean rate of 20% (n = 80). We compared survival rates within and between years but did not detect differences between collared and uncollared ($P > 0.4$), male and female ($P > 0.2$), or singleton and twin ($P > 0.1$) calf moose.

DISCUSSION

Knowledge of both fecundity and survival of progeny is critical to understanding population dynamics within a moose population (Boer 1992). Previous work suggests that pregnancy and twinning rates may be sensitive indicators of range condition and moose population status relative to K (Franzmann and Schwartz 1986, Boer 1992). Female moose productivity in the western Yukon Flats compared favorably with moose in other areas of North America (Table 4). Our observed pregnancy rate (89%) exceeded estimates for south-central and interior Alaska (Ballard et al. 1991, Keech et al. 2000), and southern Yukon (Larsen et al. 1989) and was above the mean of North American ranges presented in Gasaway et al. (1992). Twinning rate was high (63%) and near the upper end of ranges of populations in Alaska that were reported below K (range 23%–90%; Gasaway et al. 1992) and also exceeded those reported in low-density populations in Canada (Larsen et al. 1989, Stenhouse et al. 1995). A high twinning rate infers that a population is occupying productive habitat and is not characteristic of a population strongly limited by nutrition (Van Ballenberghe and Ballard 1998).

Table 3. Annual survival estimates[a] for moose calves monitored in eastern interior Alaska, USA, 1998–2000.

Parameter	1998			1999			All years		
	n	$\bar{x}$	95% CL	n	$\bar{x}$	95% CL	n	$\bar{x}$	95% CL
All calves	39	0.15	0.04–0.27	41	0.24	0.09–0.40	80	0.20	0.10–0.30
Males[b]	15	0.20	0.00–0.40	16	0.31	0.02–0.61	31	0.26	0.08–0.44
Females	13	0.15	0.04–0.35	12	0.17	0.04–0.38	25	0.16	0.02–0.30
Singletons[c]	11	0.18	0.05–0.41	13	0.39	0.04–0.73	24	0.29	0.08–0.51
Twins	28	0.11	0.01–0.22	27	0.22	0.05–0.39	55	0.16	0.06–0.27
Collared	29	0.17	0.03–0.31	29	0.24	0.06–0.43	58	0.21	0.09–0.32
Uncollared	10	0.10	0.09–0.29	12	0.25	0.05–0.55	22	0.18	0.00–0.37

[a] Estimates derived using Kaplan-Meier method with staggered entry design (Pollock et al. 1989).
[b] One calf 1998, 1 calf 1999, gender not determined.
[c] One calf 1999, unknown if singleton or twin.

Table 4. Known fate and annual survival rates of moose calves and reproductive statistics from low-density moose populations in North America. Reprod. = reproductive, Preg. = pregnancy.

Population	Population density (per 1,000 km²)	% Reprod. rates		% Annual survival rates (n)		% Calf mortality rates (n)					Reference
		Twin	Preg.	Cow	Calf	Black bear	Grizzly bear	Wolf	Drown	Other	
Eastern Interior, AK	120–180	63	89	88 (55)	20 (80)	45 (17)	39 (15)	3 (1)	8 (3)	5 (2)	This study
Mackenzie Valley, NWT	140–160	31	96	85 (60)	44	—	—	—	—	—	Stenhouse et al. 1995
Mosquito Flats, AK	127–188	52	100	91 (38)	18–21 (33)	4 (1)	64 (17)	17 (5)	15 (4)	—	Gasaway et al. 1992
Lower Nowitna drainage, AK	210	53	—	—	32 (89)	62 (34)	4 (2)	18 (10)	3 (2)	13 (7)	Osborne et al. 1991
Southern Yukon	139	28	84	91 (108)	19 (117)	5 (4)	58 (49)	25 (21)	8 (7)	4 (3)	Larsen et al. 1989

We infer from fecundity parameters that the western Yukon Flats population likely is below K.

Assessment of body condition can provide insight into the ability of individuals in a population to survive and reproduce (Stephenson et al. 1999). A comparison of rump fat thickness and ingesta-free body fat from this study with other Alaska studies indicated comparable body condition indices with adult moose captured on the Tanana Flats, a high-density interior Alaska population of about 1,100 per 1,000 km² (Keech et al. 2000), but moose in the south-central, southwest, and other areas in interior Alaska displayed greater measurements (range 30 to 180%; Stephenson et al. 1999). The lower fat reserves for cows in our study may suggest a nutritional limitation when compared with other areas of Alaska; however, this comparison is made with caution due to the unknown status of each population relative to K, varying densities, and the relatively small sample size in our study ($n = 12$).

The mean total length of adult female moose in this study (305 mm) was high compared to measurements taken in 7 other Alaskan moose populations that were increasing (range of means 289 to 315; Franzmann and Schwartz 1983, Boertje et al. 1987, Gasaway et al. 1992). Body mass of neonates also was noticeably higher compared with other areas in Alaska. Mean birth mass of singleton and twin calves (19.1 kg and 16.8 kg, respectively) were greater than that described in south-central (16.2 kg and 13.5 kg, respectively; Schwartz and Hundertmark 1993) and interior Alaska (16.9 kg and 13.7 kg, respectively; Boertje

et al. 1999). We interpret the large body mass of adult females and their young as ancillary evidence that range quality may not be a significant limiting factor of population growth. A qualitative assessment of range could provide valuable information on this population's position relative to K and provide insight into apparent low fat reserves in adult cow moose.

The mean annual survival rate (88%) for adult female moose was slightly lower than in most other hunted populations in North America (range 91 to 95%; Larsen et al. 1989, Ballard et al. 1991, Gasaway et al. 1992, Keech et al. 2000), but was higher than the Mackenzie Valley in Northwest Territories, Canada (85%; Stenhouse et al. 1995). Although wolf and grizzly bear densities in the study area were estimated as low (4 and 10, respectively, per 1,000 km²), in combination, they removed 7 and 16% of radiocollared adult female moose annually in 1998 and 1999, respectively. Although resident caribou are present in low densities south of the study area and migratory herds occasionally occur near the northern and western edges of the study area, the availability of caribou generally is low. Given the high proportion of predators to prey, adult female moose survivorship may be negatively influenced by the lack of abundant alternate ungulate prey in the study area.

Predation was responsible for 92% of known moose calf mortality in this study. Black bears (45%) and grizzly bears (39%) were the major causes of mortality (Table 4). Bear predation also accounted for most predation in other studies in interior Alaska (Osborne et al. 1991, Gasaway et
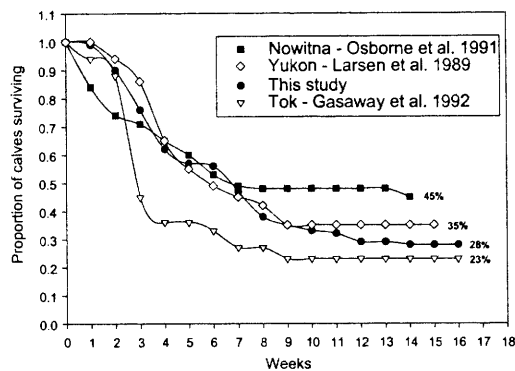
Fig. 4. Survival rates for calf moose through the first 14 weeks of life from 5 areas in North America with low moose population densities.

al. 1992, Keech et al. 2000), south-central Alaska (Franzmann et al. 1980; Franzmann and Schwartz 1986; Ballard et al. 1981, 1990, 1991), and southern Yukon (Larsen et al. 1989). Although wolf predation has been found to be an important source of neonatal predation in other studies in Alaska (Gasaway et al. 1992, Keech et al. 2000) and southern Yukon (Larsen et al. 1989), only 1 neonate was killed by wolves in our study. Bear predation was evenly distributed between black bears and grizzly bears, similar to the pattern observed by Keech et al. (2000). Hair sample analyses (n = 18) from mortality sites indicated >94% of black bears were males. Despite low estimated densities of grizzly bears in this region, they were a significant predator on both neonate and adult moose. Our data support the conclusions of Larsen et al. (1989), who indicate that grizzly bears may be the most effective of the 3 predators (black bear, grizzly bear, wolf) and can have significant impacts on moose populations even when bears occur at low densities.

Mean annual calf survival (20%) was similar to rates reported from Mosquito Flats, Alaska (Gasaway et al. 1992), and southern Yukon (Larsen et al. 1989; Table 4). Higher survival rates (32 to 53%) have been reported in other studies (Ballard et al. 1981, 1991; Franzmann and Schwartz 1986; Osborne et al. 1991; Keech et al. 2000). We documented low neonatal survival (28%) through the first 14 weeks of life, similar to other studies (range 23–45%, Fig. 4) of low-density moose populations. An additional 8% of the calves died between 2.5 and 5 months of age, but overwinter mortality was low (n = 1). We did not

detect a difference in survival rates for singletons and twins, unlike previous studies (Osborne et al. 1991), or for collared and uncollared calves.

We also examined other factors that can influence moose population growth, including deep snow, disease, starvation, drowning, and human harvest. Coady (1974) concluded that snow depths exceeding 90 cm restrict the movements and foraging ability of adult moose. Mean annual snow accumulation in the study area was <64 cm. Although snow accumulation in 1999 was above the mean (76 cm), we observed high overwinter calf and adult survival, and high twinning rates the following summer. Although drowning contributed to annual mortality of neonates (8%), these deaths probably were caused indirectly by predators. We did not detect drowning, disease, or starvation among collared adults. Harvest reports indicated that 7 to 12% of the population was being removed annually by hunting and at least 33% of this harvest consisted of illegal take of cows. Based on personal communications with local residents, we suspect that harvest actually is higher than reported (P. Williams, Beaver resident, personal communication). Although cow harvest is illegal, it is a traditional activity practiced by many local hunters and contributes significantly to total annual harvest. Population surveys indicate that annual moose harvest may be nearly equal to prewinter yearling recruitment. Our limited data suggest that low calf survival, adult mortality from wolf and grizzly bear predation, illegal cow harvest, and low predator harvest, all act in concert to maintain this moose population at a low density. Despite these limiting factors, the population's high reproductive rate and relatively high overwinter survival rates of calves and adult females reduce the chance that the population will decrease to even lower densities.

MANAGEMENT IMPLICATIONS

Our data identified some of the factors that limit population growth in a low-density moose population within a multiple-predator system. We also described reproductive and fitness indices for adult female and neonate moose which allowed us to make inferences on the population's status with respect to K. The characteristics of this population closely fit the low-density dynamic equilibrium model (LDDE) described by Gasaway et al. (1992). The LDDE model pertains to populations that include lightly harvested wolf and bear populations, low moose densities that fluctuate over time

but remain below *K*, and moose as the primary prey. This population also received significant illegal harvest of cow moose. Management of low-density moose populations can be challenging when the public perceives that the role of managers is to change predator populations to increase prey populations. Tools that were traditionally used by hunters and managers to effectively alter predator densities and boost prey densities—i.e., aerial hunting and government-sponsored predator-removal programs—are no longer acceptable to the public. Conventional methods such as public hunting and trapping of predators, liberalizing seasons and bag limits, trapper and hunter education, and increased law enforcement must be used and modified to increase their effectiveness. Perhaps the greatest challenge is providing adequate incentives for trappers and hunters to increase predator harvest. The first step to effectively manage predator–prey populations is to facilitate implementation of a conservation plan. Cooperative efforts must be initiated between local users, tribal and village governments, state and federal managers, and other stakeholders to identify predator–prey population management goals and strategies to achieve these goals. We believe that only by establishing a citizen-based advisory group comprised of resource users and utilizing a consensus decision-making process will managers be successful in effecting change in predator and prey populations.

ACKNOWLEDGMENTS

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