

LIFE-HISTORY CONSEQUENCES OF MATERNAL CONDITION IN ALASKAN MOOSE

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Abstract: We studied life-history characteristics of Alaskan moose (*Alces alces gigas*) including the effects of maternal condition of adult females (>33 months old) on survival and physical condition of young during their first year-of-life. We also examined the relation between maternal condition and reproductive parameters of individual adult moose, and tested for effects of those parameters on timing and synchrony of parturition. We radiotracked adult females captured in both March 1996 and 1997 throughout the year with intensive monitoring occurring during spring and early summer. That procedure enabled us to capture the offspring of females we monitored and record other variables related to reproductive success. Females with greater rump fat thickness had higher rates of pregnancy, gave birth to more twins, and produced young with higher birth masses than did females with less rump fat. Time-to-death for individual young increased as birth mass increased and decreased as birth date and litter size increased; those birth variables, however, did not act upon time-to-death independently. Our results indicated maternal condition influenced subsequent variables associated with birth, which ultimately affected future survival of offspring. Further, timing of reproduction varied between the 2 years, with births occurring earlier but not more synchronously in 1996 than in 1997. Time of parturition occurred earlier for individual females with the thickest rump fat. That outcome indicated that timing of parturition was the result of environmental factors acting on females prior to giving birth rather than effects of attempting to avoid predation.

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Survivorship of young has been implicated as a critical density-dependent mechanism regulating populations of ungulates (Klein 1968, McCullough 1979, Clutton-Brock et al. 1987, Kie and White 1985, Bartmann et al. 1992, Sams et al. 1996). Although proximate causes (predation, disease, drowning, malnutrition, and adverse weather) of juvenile mortality may vary, maternal malnutrition is thought to be a predisposing factor for mortality in high-density populations (Carroll and Brown 1977, Wilson and Hirst 1977, Clutton-Brock et al. 1987). For individuals in relatively poor physical condition, weather can produce variation among years in life-history variables (McCullough 1979, Langvatn et al. 1996, Bowyer et al. 2000). For ex-

ample, a moose population existing at high density with respect to its habitat may suffer greater effects from adverse weather (Peterson and Page 1983, Messier 1995). Nonetheless, the importance of density dependence under natural conditions is still debated (McCullough 1990, Bowyer et al. 1999a), particularly in predator-rich environments (Van Ballenberghe and Ballard 1994, 1998).

Studies of ungulates have demonstrated a relationship between physical condition of females and survival of juveniles (McCullough 1979, Clutton-Brock et al. 1987, Bartmann et al. 1992, Cameron et al. 1993, Testa and Adams 1998). Likewise, the effect of variables related to physical condition of young at the time of birth also can influence subsequent survival of young (Clutton-Brock et al. 1987, Whitten et al. 1992, Fairbanks 1993, Sams et al. 1996, Singer et al. 1997, Smith and Anderson 1998).

We investigated the relationship between

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physical condition of females and condition of their offspring, and attempted to elucidate the role of those factors in effecting survival of the offspring in a relatively high-density population of moose (Keech et al. 1998). We hypothesized condition of offspring and timing of parturition would be directly related to the physical condition of the female. We also hypothesized condition of offspring would be directly related to their subsequent survival. Likewise, we predicted that survival of young would be influenced by the condition of the female via her investment in offspring. Finally, we examined the role of environmental conditions and predation in determining timing and synchrony of parturition. We predicted that if timing of parturition was related primarily to predation (Estes 1976, Estes and Estes 1979, Festa-Bianchet 1988), young moose born at the peak of the birthing distribution should have the highest survivorship (Bowyer et al. 1998b). Conversely, if the primary factor regulating timing of parturition was the need to maximize use of the short growing-season in the sub-Arctic (Rachlow and Bowyer 1991, Bowyer et al. 1998b), early born young should exhibit greater survivorship than those born later.

STUDY AREA

We studied moose in a 6,730-km² area of interior Alaska (64°18'N, 147°45'W) between the Tanana River and the Alaska Range, about 25 km south of Fairbanks, Alaska, United States. This area encompasses a large portion of the Tanana Flats and the foothills of the northern Alaska Range described previously by Gasaway et al. (1983). The portion of the study area between 130 and 1,200 m in elevation contains most habitats used by moose. The area consists primarily of mountain valleys and foothills to the south, and sprawling, poorly drained lowlands to the north (the Tanana Flats).

Fire has played a dominant role in the creation of a mosaic of vegetation within these lowlands, resulting in a mix of shrub, young spruce (*Picea sp.*) forest, climax bogs, and older stands of black spruce (*Picea mariana*; Gasaway et al. 1983, Gasaway and Dubois 1985). Vegetation in the foothills and mountains grades from taiga, consisting of white spruce (*Picea glauca*), black spruce, paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*) at low elevations, to shrub communities of willow (*Salix sp.*), dwarf birch (*B. glandulosa* and *B. nana*),

and alder (*Alnus*), with alpine tundra occurring at high elevations (LeResche et al. 1974, Gasaway et al. 1983).

The climate is typical of interior Alaska. Temperatures frequently reach 25°C in summer and often fall to -40°C in winter. Mean depth of snow is generally <70 cm, and usually remains dry and loose throughout winter (Gasaway et al. 1983). Mean depth of snow on the ground at the Gold King weather station was 36 cm in February, and 38 cm in April 1996. Data for 1997 exhibited a similar pattern (Feb = 46 cm, Mar = 48 cm, Apr = 46 cm); other months were not available (Natural Resources Conservation Service, Anchorage, Alaska, unpublished data). Snow depths >80 cm typically are necessary to influence survivorship of young moose (Gasaway et al. 1983).

Moose within our study area occur at a crude density of 1.1 moose/km² and are increasing (Keech et al. 1998). This density is high compared with other areas of interior Alaska, where populations are held at low levels by predation (Gasaway et al. 1992, Molvar et al. 1993, Van Ballenberghe and Ballard 1994, Boertje et al. 1996). Female moose are sexually segregated from adult males during winter and around parturition (Miquelle et al. 1992, Bowyer et al. 1997), and seclude themselves from other moose prior to giving birth (Bowyer et al. 1999b), which facilitated our capturing female-young pairs. Large carnivores inhabiting the study area include wolves (*Canis lupus*), coyotes (*C. latrans*), black bears (*Ursus americanus*), grizzly bears (*U. arctos*), wolverines (*Gulo gulo*), and lynx (*Lynx canadensis*). In addition to moose, other large prey for those carnivores include caribou (*Rangifer tarandus*) and Dall's sheep (*Ovis dalli*; Gasaway et al. 1983, 1992).

METHODS

Capture of Adults, Condition Indices, Radiotelemetry, and Mortality

During 1-4 March 1996, we immobilized 22 adult female moose (>33 months old) in the Tanana Flats and 22 adult female moose in the foothills of the Alaska Range. During 10-13 March 1997, we recaptured 16 moose from the Tanana Flats, and 12 moose from the Alaska Range to reevaluate condition; we captured 2 additional female moose in the Tanana Flats. We immobilized moose with 4.0-4.5 mg (1.33-1.5 cc) carfentanil citrate (Wildnil®, Wildlife

Pharmaceuticals, Fort Collins, Colorado, USA) and 150–167 mg (1.5–1.67 cc) xylazine hydrochloride (Anased®, Lloyd Laboratories, Shenandoah, Iowa, USA). The immobilizing agent was administered intramuscularly via a 3-cc projectile syringe (2.9-cm needle) fired from a Palmer Cap-Chur® rifle (Douglasville, Georgia, USA) while hovering over the moose in a 1 (Robinson R-22) or 3 (Robinson R-44) passenger helicopter. We injected 400–450 mg (8–9 cc) of naltrexone hydrochloride (Trexonil®, Wildlife Pharmaceuticals) intramuscularly to reverse the effects of carfentanil citrate. Only 1 of 74 immobilized moose died and that moose was near death from malnutrition when darted.

When moose were immobilized we (1) measured neck girth and total length along the dorsal body contour from the hairless patch on the nose to the tip of the tail, (2) measured depth of fat on the rump via ultrasonography (Stephenson et al. 1993, Keech et al. 1998, Stephenson et al. 1998), (3) extracted a lower canine tooth to determine age from cementum annuli (Gasaway et al. 1978), and (4) collected 50 cc of blood from the jugular vein. Matson's Laboratory (Milltown, Montana, USA) processed teeth for age determination. R. L. Zarnke (Alaska Department of Fish and Game, Fairbanks, Alaska, USA) processed blood, and serum was analyzed (Bio Tracking, Moscow, Idaho, USA) for pregnancy-specific protein B (PSPB) as described by Russell et al. (1998). We diagnosed the status of pregnancy using transrectal ultrasonography in 1996 for confirmation of results from PSPB. Analysis for pregnancy with transrectal ultrasonography and PSPB gave identical results for 44 moose in 1996.

We deployed Advanced Telemetry Systems (ATS, Isanti, Minnesota, USA) radiocollars (model 2–9D3). Motion-sensing switches within transmitters allowed the signal-pulse rate to double when collars remained motionless for 5 hr (mortality mode). We radiotracked adults daily in May and early June to detect births, and listened to signals from adults approximately monthly to monitor rates of mortality.

Capture of Newborns, Condition Indices, Radiotelemetry, and Mortality

We monitored collared females that were pregnant daily from fixed-wing aircraft (Piper PA-18 Super Cub) from 12 May to 3 June 1996, and from 14 May to 6 June 1997. We noted births during flights in the early morning and

captured those newborn moose in the afternoon. We captured 46 young from 14 May to 3 June 1996, 28 young from radiocollared females and 18 young from unmarked females. From 16 May to 9 June 1997, we captured 45 young, 25 from radiocollared females and 20 from unmarked females. Mean age of newborns captured from radiocollared females was 1.5 days and all were <6 days old. Likewise, the mean age of young captured from unmarked females was estimated at 3 days and no newborns were estimated to be >9 days old.

We captured newborn moose using a Jet Ranger 206 helicopter during 1996 and an R-44 helicopter in 1997, using techniques described by Ballard et al. (1979). Once the female was separated from her young, the capture crew caught neonates by hand. We released young in <5 min to minimize separation time between the female and her offspring. We used latex gloves and individual weighing and restraint bags (nylon bushel bags) to minimize transfer of scent, although human scent is not likely a problem in rebonding of mother and young in cervids (Bowyer et al. 1998a). When twins were present, we captured and restrained both young but processed only 1 and released both simultaneously.

We determined sex of young and weighed individuals to the nearest 0.5 kg by placing them in a bag and suspending them with a 25-kg Chatillon (Kew Gardens, New York, USA) spring scale. We collected 3 cc of blood from the jugular vein. To estimate birth masses, we subtracted 1.6 kg for each day >0.5 days old. That correction factor was based on regression models using masses of known-age young. We omitted young estimated at >6 days old from regression analysis involving birth date because of uncertainty in estimating that parameter. Additionally, for analyses involving just birth mass, only those individuals estimated to be <4 days old were used.

During 1996, we deployed radiocollars weighing 180 g each (ATS model 8 transmitters, 1.5-hr motion-sensing switch) constructed from 2 layers of 10-cm PEG® (Franklin Lakes, New Jersey, USA) elastic bandage to allow the collar to expand and eventually fall off (Osborne et al. 1991). During 1997, we used radiocollars (200 g) constructed from 4 layers of elastic bandage. The day following capture we visually located young with radiocollars to assure they rebonded with their mother. Following visual confirma-

Table 1. Summary statistics for depth of rump fat for nonpregnant, pregnant, singleton-producing, and twin-producing adult female moose, March 1996 and 1997 in interior Alaska, USA.

Status of adult females	Rump fat at midpoint (cm)			Rump fat at maximum (cm)		
	\bar{x}	SE	n	\bar{x}	SE	n
Nonpregnant	0.05* ^a	0.04	8	0.33*	0.20	8
Pregnant	0.55*	0.01	64	1.44*	0.12	65
Producing singletons	0.51***	0.06	42	1.29**	0.14	42
Producing twins	0.81***	0.13	11	2.16**	0.27	12

^a Depth of rump fat differs significantly (*t*-test) between categories of adult females at * ($P \leq 0.001$), ** ($P \leq 0.01$), and *** ($P \leq 0.05$).

tion of rebonding, we listened to signals of young to determine their survival. Flights were conducted daily until 13 June, and every other day until 30 June, after which the tracking interval gradually increased to twice each month during winter. We investigated mortality signals immediately using a helicopter to locate young. We used criteria and techniques described by Ballard et al. (1979) and Adams et al. (1995), involving examination of carcasses and mortality sites for tracks, feces, hair, tooth marks, and other signs to evaluate causes of death.

Eleven young from the 1996 cohort lost their collars (8 from collared females, and 3 from uncollared ones). We censored those young from uncollared females, but visually located collared females to evaluate mortality rates of their young. If the young were not with the collared female on 3 consecutive flights, we assumed the young had died. No young from the 1997 cohort lost their collars.

Statistical Analyses

Two-tailed *t*-tests with pooled variances were used to examine differences in rump-fat depths and to test for differences in birth mass between years, sexes, and litter sizes (Zar 1996: 93). We used simple linear regression to evaluate whether relationships existed between birth date and depth of rump fat. We tested for differences among median dates of births between years and between litter sizes using the 2-sample median test (Zar 1996:157). The Smirnov test (Conover 1980:369) was used to determine whether birthing distributions differed between 1996 and 1997. Proportions were compared with the *z*-test (Remington and Schork 1970:217). Sources of mortality between 1996 and 1997 were compared with the chi-square test (Conover 1980:153).

We estimated survivorship of young moose at 30-day intervals using the Kaplan-Meier procedure (Pollock et al. 1989). We also estimated

failure-rate models for time-to-death for young moose using parametric Weibull regression with PROC LIFEREG (SAS Institute 1996). Survival analysis, failure rates, and hazard models are related by the equation: hazard function = time to failure/survival function. Parametric failure-rate models can be appropriate for wildlife studies if they are applied carefully (White and Garrott 1990:243). Additionally, parametric analysis of survival data may be superior to nonparametric analysis if assumptions are satisfied (Efron 1988); parametric methods also deal with covariates and interactions better than nonparametric methods such as the Kaplan-Meier procedure. We assumed a Weibull error distribution for the regression because that method provided a flexible proportional-hazards model that naturally scaled hazard rates that depended on covariates. We used PROC LIFEREG to construct a model that best explained the influence of the independent variables related to neonatal condition (birth mass, birth date, litter size, sex, and birth year) on time-to-death (e.g., survivorship). Additionally, PROC LIFEREG was used to model the influence of the independent variables potentially associated with female condition (female age, maximum depth of rump fat, midpoint depth of rump fat, and wintering area) on time-to-death for their young. Time-to-death was modeled from birth to 365 days old. As a diagnostic, we compared results from Kaplan-Meier analysis (Pollock et al. 1989) with fitted parametric estimates for all data in the absence of covariates, and thereby judged the parametric model to be reasonable.

RESULTS

Age Structure, Reproduction, and Rump Fat of Adult Females

Mean age of an adult female was 6.8 years ($SE = 0.5$ yr, range = 2–13 yr, $n = 45$) in 1996. Because the same moose were sampled in 1997,

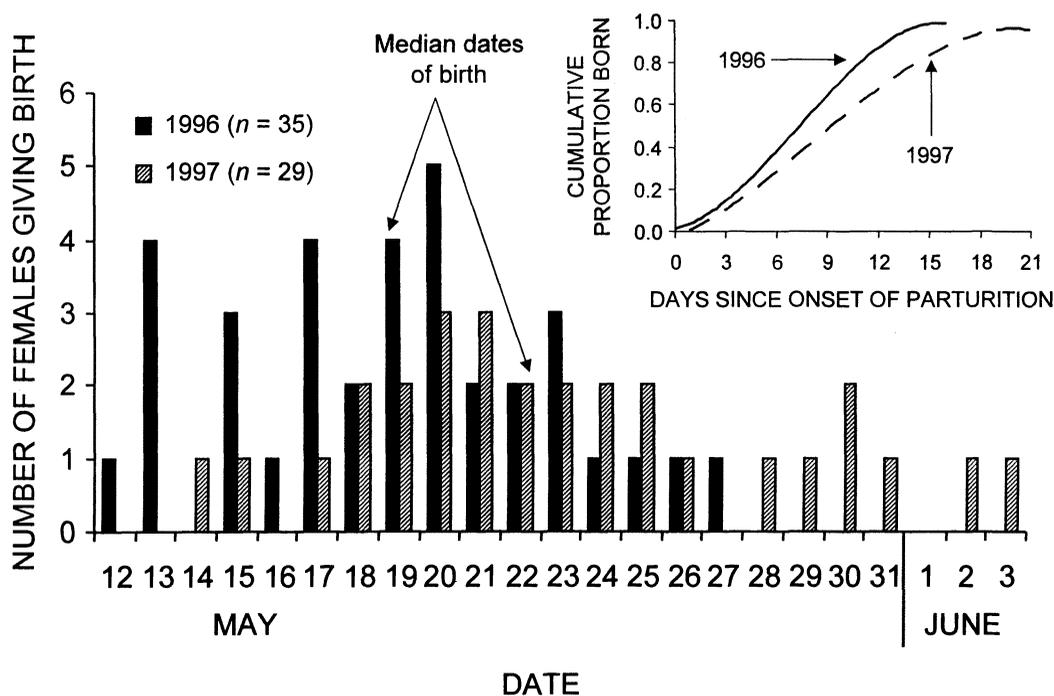


Fig. 1. Timing and synchrony (inset) of parturition for female moose in interior Alaska, USA, during 1996 and 1997.

females were on average 1 year older. In 1996, 98% of 44 adult females were pregnant, and in 1997 the pregnancy rate was 77% of 30 adults; difference between years was significant ($Z = 2.31$, $P = 0.02$). Twinning occurred in 31% of 35 births in 1996 and 10% of 29 births in 1997, which also differed ($Z = 2.18$, $P = 0.03$).

Both mean (\pm SE) midpoint and maximum depth of rump fat were greater (t -test, $P < 0.01$) in 1996 (0.6 ± 0.06 cm, $n = 42$; 1.6 ± 0.15 cm, $n = 43$) than in 1997 (0.4 ± 0.04 cm, $n = 30$; 1.0 ± 0.16 cm, $n = 30$). Maximum depth of rump fat was significantly greater among preg-

nant than nonpregnant females ($t = -4.72$, $df = 12.9$, $P = 0.001$; Table 1). Maximum depth of rump fat also was significantly greater for females giving birth to twins versus those with singletons ($t = -2.88$, $df = 52$, $P = 0.006$; Table 1). Regression indicated no relationship between depth of rump-fat and age of adult females ($r^2 = 0.0004$, $df = 72$, $P = 0.87$).

Timing of Parturition, Birth Mass, and Relations with Rump Fat

During 1996, 35 births of radiocollared females were observed between 12 and 27 May,

Table 2. Summary statistics for mass of newborn moose capture during May 1996 and 1997 in interior Alaska, USA. No male twins were captured in 1997.

Year	Singleton						Twin					
	Birthweight ♂ (kg)			Birthweight ♀ (kg)			Birthweight ♂ (kg)			Birthweight ♀ (kg)		
	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE	N
1996 ^a	18.9	0.95	10	16.4	0.63	17	14.1	1.20	4	13.5	0.57	6
1997 ^a	17.6	0.57	15	16.2	0.50	21				14.4	0.64	3
Combined (1996-97)	18.1	0.54	25	16.3	0.39	38	14.1	1.20	4	13.8	0.43	9

^a No significant difference between years ($P > 0.2$) within sex or sibling groups; t -test.

^b Mean birth mass for male versus female singletons were significantly different in 1996 ($P = 0.04$), 1997 ($P = 0.08$), and combined 1996-97 ($P = 0.01$); t -test.

^c Mean birth mass of singleton and twin males were significantly different in 1996 and combined 1996-97 ($P = 0.02$ and 0.01 , respectively). Mean birth mass of singleton and twin females were significantly different in 1996 and combined 1996-97 ($P = 0.02$ and 0.005 , respectively); difference not significant (t -test) in 1997 ($P = 0.21$).

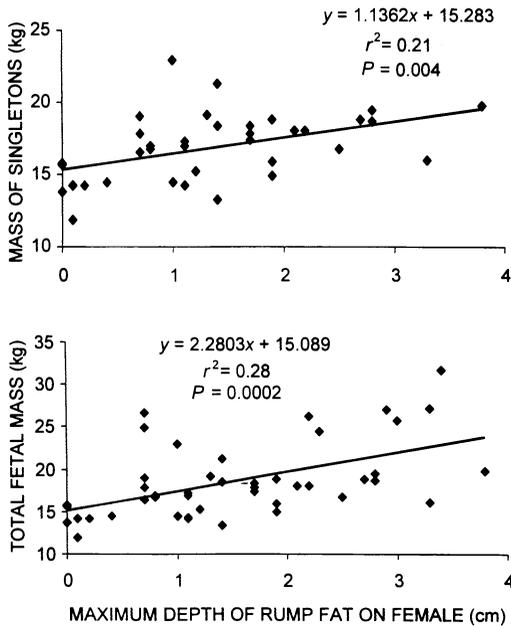


Fig. 2. Relationship between depth of rump fat of female moose in March and birth mass of singleton newborns ($n = 37$), and between depth of rump fat and total fetal mass ($n = 45$), interior Alaska, USA, 1996 and 1997.

with 80% of births occurring within 11 days and 95% of births within 14 days; median date of birth was 19 May (Fig. 1). During 1997, 29 births of radiocollared females were observed between 14 May and 3 June, with 80% of births occurring within 13 days and 95% of births within 20 days. In 1997, the median birth date was 22 May (Fig. 1). Distribution of births approximated normality and were skewed slightly right (Fig. 1). Timing of parturition for radiocollared females was significantly different in

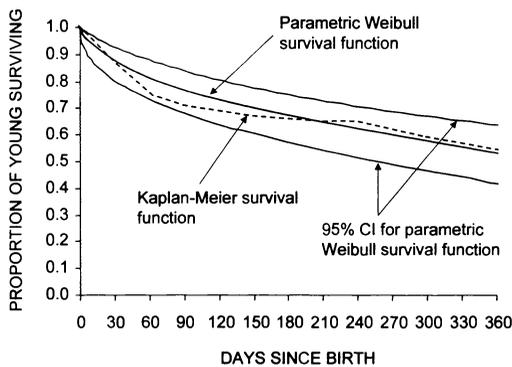


Fig. 3. Parametric survival curve (error distribution = Weibull) for young moose from birth to 365 days old in interior Alaska, USA, 1996 and 1997 ($n = 81$).

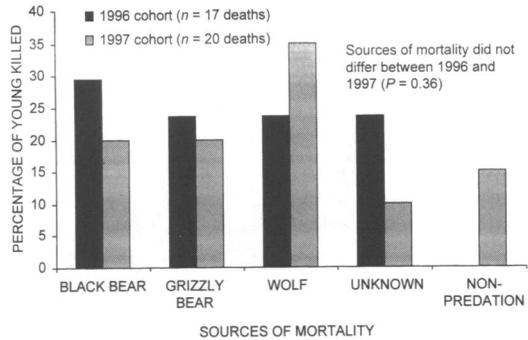


Fig. 4. Sources of mortality for young radiocollared moose that died during 1996 and 1997 in interior Alaska, USA.

1996 and 1997 (2-sample median test, $P < 0.05$). Timing of parturition for females giving birth to singleton or twin young was not different (median date of birth = 21 May and 20 May, respectively; 2-sample median test, $P > 0.9$). Likewise, synchrony of births (Fig. 1,) did not differ between years (Smirnov 2-sample test, $P > 0.2$).

Mean birth mass was $13.7 \text{ kg} \pm 0.41 \text{ kg}$ ($n = 15$) for twins and $17.0 \text{ kg} \pm 0.32 \text{ kg}$ ($n = 66$)

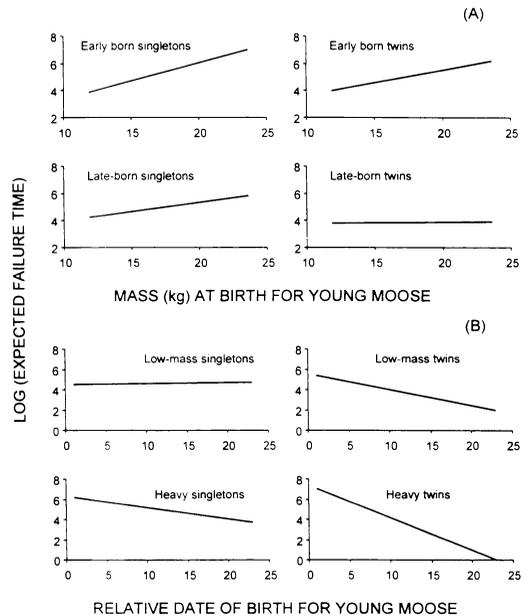


Fig. 5. Relationship between birth mass (A), birth date (B), litter size, and log of expected failure time (death), for 81 moose captured as newborns in interior Alaska, USA, during May 1996 and 1997. Categories for young include low-mass (mass at birth = 14.5 kg), heavy (mass at birth = 18.1 kg), early born (relative birth date = day 7, or 1/3 through the birthing distribution), and late born (relative birth date = day 11, or 2/3 through the birthing distribution).

for singletons. Individual twins weighed significantly less than singletons (males and females pooled, $t = 4.67$, $df = 79$, $P < 0.0001$) and female singletons weighed significantly less than did their male counterparts ($t = -2.82$, $df = 61$, $P = 0.007$; Table 2).

Regression analysis indicated a significant ($P = 0.04$) negative relationship (slope = -1.355) between birth date and maximum depth of rump fat in March. We also tested for an interaction between depth of rump fat and year, but that term was not significant ($P = 0.5$). Therefore, we pooled years giving a model with a common slope but separate intercepts. We also observed that the fattest females produced, on average, the heaviest offspring. Regression analysis indicated that birth mass of singletons was positively related to rump fat of females in March ($r^2 = 0.21$, $df = 36$, $P = 0.004$). Total fetal mass (same as birth mass for singletons and 2 times birth mass for twins) also was related positively to rump-fat of females ($r^2 = 0.28$, $df = 44$, $P = 0.0002$; Fig. 2).

Mortality

In 1996 we did not detect births for 15% of 41 pregnant females, and in 1997 for 13% of 23 pregnant females; this difference was not significant ($Z = 0.02$, $P > 0.9$). These females were determined previously to be pregnant during March based on both transrectal ultrasonography and PSPB analyses in 1996 and PSPB analysis only in 1997. This change in pregnancy rate may be accounted for by perinatal mortality (mortality that occurred during the first 24 hr after birth), intrauterine mortality (mortality occurring between the diagnosis of pregnancy in March and the birthing period), or incorrect diagnosis of pregnancy.

During the first year (1 Mar 1996–28 Feb 1997), predators killed 7% of 44 radiocollared adult females. Wolves killed 1 female between late April and mid-May 1996, and 1 female during November 1996. A grizzly bear killed 1 female during June 1996. Additionally, a trapper accidentally killed 1 female during January 1997. During the second year (1 Mar 1997–28 Feb 1998), predators killed 5% of 43 adult female moose. Wolves killed both of those moose during March 1997. In addition, 1 malnourished female died following recapture in early March 1997.

We collared 91 newborn moose during 1996 and 1997. Eight young died from capture-in-

duced reasons (trampling by female or abandonment following release), and we eliminated those individuals from the survival analyses. We observed 2 stillbirths (1 each in 1996 and 1997), 1 from a set of twins and 1 singleton.

Radiocollared young experienced a high annual rate of survival (53%; Fig. 3) and survival of young did not differ between years ($P > 0.5$). Predation was the major proximate cause of death in young, with wolves, grizzly bears, and black bears killing about equal proportions of young (Fig. 4). Nonpredation mortality was attributed to drowning, malnutrition, and injuries inflicted by other moose.

Relations Between Neonate Condition, Female Condition, and Mortality of Young

We studied the relationship between survival of young to 1 year-of-life and birth year, birth mass, birth date, litter size, and sex. Analysis of those data with parametric regression provided the following model: $\log(\text{expected time-to-death}) = -4.485 + 0.718 \text{ birth date} + 1.546 \text{ litter size} + 0.727 \text{ birth mass} - 0.049 \text{ birth mass} \times \text{birth date} - 0.017 \text{ birth mass} \times \text{birth date} \times \text{litter size}$. Birth year and sex did not enter the model at $P > 0.15$. That model indicated that expected time-to-death (e.g., survivorship) for young moose was inversely related to birth date and litter size, and positively related to birth mass, although interactions occurred among those variables. For instance, the expected time-to-death for newborns increased as birth mass increased (Fig. 5A), but the differing rate of increase in each category (early born singleton, early born twin, late-born singleton, late-born twin; Fig. 5A) partly explained interactions that occurred between birth mass and birth date, and birth mass and litter size. For example, the relatively flat slope produced by late-born twins indicated that their survival was not influenced by their size at birth, whereas a singleton that was born late experienced some benefit from increased body mass. Likewise, the expected time-to-death typically decreased as birth date increased for newborns (Fig. 5B).

We also studied the relationship between survival of young to 1 year old and female age, measures of female rump-fat depth, and wintering area. Analysis of those data using parametric regression indicated that none of those variables entered the model ($P > 0.15$) predicting time-to-death.

DISCUSSION

We demonstrated that condition of female moose drastically effected timing of reproduction and other life-history patterns of their young. The age structure of female moose in spring 1996 indicated that our study population was well represented by young and middle-aged moose (2–8 yr), which was characteristic of good recruitment into the population (Van Ballenberghe and Ballard 1998). Aerial surveys conducted by the Alaska Department of Fish and Game indicated the population had increased during our study. Although we are uncertain where the population was relative to ecological carrying capacity (K), moose in our population were approaching the upper limits of density reported by Gasaway et al. (1992).

Caution should be used in making inferences concerning K across populations of moose from density alone; K may vary with differences in habitat quality among populations (Weixelman et al. 1998, Bowyer et al. 1999a). Nonetheless, several lines of evidence, in addition to increasing population size, indicated that moose inhabiting our study area were experiencing some density-related effects on their life-history characteristics (sensu McCullough 1999). Survivorship of young (Fig. 3) was >0.85 after their first month-of-life; comparative data for a low-density population of moose in the nearby foothills of the Alaska Range that was limited by predation exhibited survivorship (0.20) that was much lower (Bowyer et al. 1998b). Indeed, such low survivorship of young is typical of predator-regulated populations in Alaska (Ballard et al. 1981, Boertje et al. 1988, Osborne et al. 1991), including previous data for moose inhabiting our study area (Gasaway et al. 1983, 1992). That young moose did not experience low survivorship (Fig. 3) resulting from compensatory mortality expected near K (McCullough 1979) is ancillary evidence that the population had not yet reached or overshot K .

Pregnancy rates of moose within our study area declined significantly between years (98 vs. 77%). Likewise, those adult females exhibited relatively low rates of twinning (31 vs. 10%) that also declined significantly. Again, those data for twinning were much lower than for the low-density population of moose in the nearby Alaska Range, which varied between 32–64% twins over 5 years (Bowyer et al. 1998b). Indeed, moose populations below K tend to exhibit high

rates of pregnancy and reproduction (Boer 1992, Gasaway et al. 1992), whereas individuals in poor physical condition, which would be expected near K , have a decreased probability of becoming pregnant and reproducing successfully (Heard et al. 1997, Schwartz 1998). Pregnancy and twinning rates are regarded as indicators of range condition and productivity in populations of moose (Franzmann and Schwartz 1985, Schwartz and Hundertmark 1993, Bowyer et al. 1998b).

Population dynamics of moose are thought to be influenced by density-dependant processes (Van Ballenberghe and Ballard 1998). Such processes relate to intraspecific competition and ultimately to the physical condition of females, and thereby to their reproductive success (Schwartz and Hundertmark 1993). Indeed, 2 recent publications indicated that populations of moose exhibited strong density-dependant mechanisms (Bowyer et al. 1999a, Hjeljord and Histol 1999). Although we cannot test hypotheses concerning density dependence with 2 years of data, increasing population size, high density relative to other populations in interior Alaska, decreasing fat reserves of females, declining pregnancy rates, and low twinning rates, makes density dependence the most likely and only consistent explanation of our data for moose inhabiting the study area.

Winter weather also would be expected to interact with population density and consequently influence reproductive characteristics of moose (Bowyer et al. 1998b, Hjeljord and Histol 1999). Females at low density and in excellent physical condition are likely well buffered against harsh winter conditions (Bowyer et al. 1998b), whereas females experiencing poor nutrition resulting from intense intraspecific competition at high density would be more susceptible to the effects of severe weather (Bowyer et al. 2000).

Winter conditions within our study area were mild with <50 cm of maximum snow depth accumulating during both 1996 and 1997; depth of snow is thought to be far more important than temperature in affecting energy expenditures of moose during winter (Bowyer et al. 1997). Moreover, depth of snow (36–48 cm) was less than the 50–90 cm that Bowyer et al. (1998b) reported as having no effect on twinning rate in the Alaska Range, and is likewise below the 70 cm mark reported to begin restricting travel of moose (Kelsall 1969, Coady 1974). Likewise, Bowyer et al. (1999a) failed to

find relationships among reproductive parameters for moose and weather variables where winters were mild. We cannot directly compare reproductive performance of moose and winter weather with only 2 data points. Previous studies indicate, however, that winter conditions during our study were too mild to markedly affect our results.

Predation was the proximate cause of most mortality for young moose in our study. Past research also has documented high rates of predation on young moose. Black bears, grizzly bears, and wolves all have been identified as principle predators on young (Franzmann and Schwartz 1980, Ballard et al. 1981, Gasaway et al. 1983, Boertje et al. 1988, Larsen et al. 1989, Osborne et al. 1991). Unlike that previous research, mortality in our study was evenly distributed between black bears, grizzly bears, and wolves (Fig. 4) at a low overall rate (Fig. 3). We acknowledge, however, that survivorship in high-density populations likely is related to physical condition, and that compensatory mortality of young may occur if our study population continues to increase.

Whatever the cause of the decreased physical condition of female moose in our study population, we demonstrated a direct link between maternal condition and condition of offspring; those variables hold the potential to affect life-history characteristics of this large cervid. We noted the fattest females produced the heaviest newborns (Fig. 2). Additionally, both pregnancy and litter size of adults were significantly related to depth of rump fat in March (Table 1). Female moose giving birth to twins were in better condition than those giving birth to singletons. Our findings are consistent with relationships reported between twinning rates of moose and both mass of kidney fat (Heard et al. 1997) and pregnancy of yearling females (Boer 1992).

The correlation we noted between female condition and pregnancy rates agrees with results reported by Testa and Adams (1998) who measured depth of rump fat in early winter. Further, we observed a significant relationship between rump fat in March and birthing date. Females in better condition gave birth earlier. Testa and Adams (1998) reported a similar relationship between birth date and fat depth of females for birth of singletons. Those relationships provided a direct link between female condition and reproductive investment. Birth mass, pregnancy rate, litter size, and birth date

all have been used as indices to describe density or weather-related effects on ungulates (McCullough 1979; Gasaway et al. 1983; Franzmann and Schwartz 1985; Rachlow and Bowyer 1994, 1998). The relationships we have observed between female condition and reproductive investment further confirm those well-established measures.

To determine if condition of young moose at time of birth would influence their future survival, we tested whether survivorship could be explained, in part, by birth variables. Previous research has shown that early survival of northern cervids can be influenced in predator-rich environments by sex (Smith and Anderson 1998, [elk, *Cervus elaphus*]), birth date (Adams et al. 1995, [caribou]; Singer et al. 1997, Smith and Anderson 1998, [elk]), birth mass (Whitten et al. 1992, [caribou]; Singer et al. 1997, [elk]), and litter size (Osborne et al. 1991, Stephenson and Van Ballenberghe 1995, [moose]).

Our results showed time-to-death (i.e., survivorship) was not related to sex of an individual neonate or its year of birth. Time-to-death, however, was related to birth date, birth mass, and litter size. Modeling time-to-death with parametric procedures enabled us to determine the importance of individual effects and their interactions. Because of significant interactions between birth date, birth mass, and litter size, interpretation of one effect on time-to-death cannot be accomplished independent of the others. Decreasing slopes (Fig. 5) indicated that later-born individuals have decreased time-to-death (i.e., reduced survivorship) for both large and small individuals. That pattern held for twins and singletons, although at each level of birth mass, time-to-death for twins was lower. Increasing slopes (Fig. 5) demonstrated that heavier-born young have increased times-to-death (i.e., greater survivorship) for particular categories of birth date. Likewise, that pattern held for twins and singletons, and twins generally experienced a lower expected time-to-death in each category.

Cameron et al. (1993) concluded that young caribou born to females in poorer condition had higher rates of mortality. Testa (1998) reported depth of fat on females varied significantly between newborn moose that live and died during their first 60 days-of-life. Sams et al. (1996) indicated that depressed development and delayed lactation predisposed young white-tailed deer (*Odocoileus virginianus*) to mortality. Fe-

males in poorer physical condition likely cannot provide for their offspring as well as females in better condition, or may fail to do so (Langenau and Lerg 1976, Rachlow and Bowyer 1994).

Modeling time-to-death with parametric regression indicated that none of our measures of female condition (age, measures of rump fat, and wintering location) were directly related to time-to-death of young moose. Nevertheless, the relationships we noted between female condition and birth mass of offspring (Fig. 2), birth date of offspring, and litter size (Table 1) suggest female condition may be a determinant of offspring survival through the effect of condition on other life-history characteristics. Each of those variables related to condition also was correlated with survival of young (Fig. 5). Consequently, based on those causal relationships, we hypothesize that female condition was an important determinant of survival of their offspring. In addition to survival, consequences of maternal condition may be expressed through the reproductive potential of offspring. Probability of pregnancy for northern ungulates has been related to body mass in caribou (Cameron et al. 1993, Gerhart et al. 1997), muskox (*Ovibos moschatus*; White et al. 1997), red deer (*Cervus elaphus*; Albon et al. 1986), and primiparous moose (Schwartz and Hundertmark 1993). If moose with low birth mass cannot compensate for small size (Keech et al. 1999), their future reproductive potential may be reduced.

Maternal condition provides a direct link to 3 factors that significantly influence survival of young and that outcome implies survival of young may be predetermined by factors acting upon the female prior to birth. With the exception of Testa (1998) and Testa and Adams (1998), who also worked with a relatively high-density population, past studies have failed to collect good indices of condition for females or their young, such as body mass or fat reserves. Additionally, study populations in which all individuals are in excellent physical condition, which may occur at lower densities, may make detecting changes in life-history characteristics we documented difficult. Indeed, the relatively high density of moose within our study area likely led to the production of more total young as well as increased variation in condition of individuals.

We drew several conclusions regarding to the role of environmental conditions and predation

in determining timing and synchrony of parturition. If predation was responsible for synchrony in parturition, survivorship of young should be highest for those individuals born during the peak of the birthing period. Likewise, survivorship also should be highest during years when parturition was most synchronous. We observed no increase in survivorship of young born during the peak of the birthing period in 1996 or 1997. Our results provide evidence that moose timed parturition to maximize the use of the growing season (Bowyer et al. 1998b); young moose born too late in spring would not have sufficient time to accrue body reserves necessary to survive harsh conditions in winter. Our model indicated that late-born young experienced reduced survival time relative to early born animals, and that small young experience reduced survival relative to heavy-born individuals (Fig. 5). This reduced survival may result from the inability of young to exhibit compensatory growth during their first summer (Keech et al. 1999).

Bowyer et al. (1998b) documented that moose did not respond to proximal changes in weather or food supply in timing parturition, rather moose based the timing of that life-history event on long-term patterns of climate that would provide hospitable conditions for rearing young. Indeed, Gasaway et al. (1983) reported a median date of birth of 21 May in 1977–78 for this same study area, which is similar to our findings (Fig. 1). Nonetheless, we documented that physical condition of adult females, ostensibly related to density-dependant processes, also can affect birth date. In the presence of stochastic variability, however, data from more than 2 consecutive years would be desirable to more adequately explore mechanisms underpinning timing and synchrony of parturition. Our results, however, support a hypothesis that maximization of summer resources influences timing and synchrony of parturition in moose.

MANAGEMENT IMPLICATIONS

Our study illustrated several effects of female condition on reproductive performance of moose for a relatively high-density population. Birth mass, pregnancy rate, litter size, and birth date, all have been used previously as indices to describe density or weather-related effects on ungulates. We observed relationships between a direct measure of female condition and each of those reproductive indices in moose. Testa and

Adams (1998) reported no relation between twinning and fat reserves of female moose, but noted their results might have been constrained by low twinning rates. Counts of twins during spring in moose populations are one of the few indices managers have to assess physical condition and ultimately nutritional status of the population (Franzmann and Schwartz 1985). Our results indicate that pregnancy, birth date, and birth mass, as well as twinning, are directly related to the condition of the female, and therefore, provide reliable indices of population condition. Further, our results indicate that some mortality of young in this population was likely compensatory. Mortality of those young predisposed to predation may offset mortality from other causes, and cannot be used alone to infer the effects of predation on a population.

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