

**LIFE-HISTORY CONSEQUENCES OF MATERNAL CONDITION IN
ALASKAN MOOSE**

A
Thesis

Presented to the Faculty of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

MASTERS OF SCIENCE

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May 1999

ABSTRACT

We studied characteristics of life-history of Alaskan moose (*Alces alces gigas*) including the effects of maternal condition of adult females 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. We found that females in better physical condition, as indexed by 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. Expected time-to-death for individual young increased as birth mass increased and decreased with increasing birth date and litter size. Our results indicated maternal condition influenced subsequent variables associated with birth, which ultimately influenced future survival of offspring. Timing of parturition also occurred earlier for individual females with greater rump-fat thickness. That outcome suggested that timing of parturition was the result of environmental factors acting on females prior to birth.

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CHAPTER 1.

LIFE-HISTORY CONSEQUENCES OF MATERNAL CONDITION IN ALASKAN MOOSE¹

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;

¹Submitted to The Journal of Wildlife Management for publication as: Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, and B. W. Dale. Life-history consequences of maternal condition in Alaskan Moose.

those birth variables, however, did not act upon time-to-death independently of one another. Our results indicated maternal condition influenced subsequent variables associated with birth, which ultimately influenced 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 greater rump-fat thickness. That outcome suggested that timing of parturition was the result of environmental factors acting on females prior to birth rather than effects of attempting to avoid predation.

Key words: Alaskan moose, *Alces alces gigas*, birth date, birth mass, maternal condition, reproductive success, parturition, survivorship, ultrasonography

INTRODUCTION

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 (Carrol 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.* in press). For example, 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), 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 physical condition of females and condition of their offspring and attempted to elucidate the role those factors play in the 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 hypothesized that survival of young was influenced by the condition of the female via her investment in the offspring. Finally, we tested 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 captured moose in a 6730-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, USA. 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).

Moose within our study area are at relatively high densities (1.1 moose/km²) for interior Alaska, 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). Gasaway *et al.* (1992) reported that no examples existed in interior Alaska or Yukon Territory where moose maintained densities > 1.2 moose/km² over a large area, suggesting the density in our study area may be nearing the upper limits for moose in interior Alaska.

The Tanana Flats vary from 130 to 300 m in elevation, and except for occasional small hills, has no substantial relief. The area is underlain by permafrost with poor drainage. This topography and drainage result in numerous small ponds and large areas of bog dominated by low shrubs. There also are numerous clear streams and several

glacier rivers. Fire has played a dominant role in the creation of a mosaic of vegetation within these lowlands, resulting in a mix of shrub and young spruce (*Picea sp.*) forest, climax bogs, and older black spruce (*Picea mariana*) forests (Gasaway *et al.* 1983, Gasaway and Dubois 1985).

In the southern portion of the study area, mountains range in elevation to 2,500 m; however, moose rarely occur above 1,200 m (tree line). 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. Snow depth is generally <80 cm, and usually remains dry and loose throughout winter (Gasaway *et al.* 1983). Weather stations operated by the U. S. Department of Agriculture (Natural Resources Conservation Service, Anchorage, Alaska) within and around our study area reported mild winters with a maximum late-winter depth of snow of 58 cm for both 1996-97 and 1997-98.

Large carnivores inhabiting the study area include wolves (*Canis lupus*), black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), and coyotes (*Canis latrans*). 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, and we captured 2 new female moose in the Tanana Flats. We immobilized those moose with 4.0 - 4.5 mg (1.33 - 1.5 cc) carfentanil citrate (Wildnil[®], Wildlife Pharmaceuticals, Fort Collins, Colorado) and 150 - 167 mg (1.5 - 1.67 cc) xylazine hydrochloride (Anased[®], Lloyd Laboratories, Shenandoah, Iowa) administered intramuscularly via a 3 cc projectile syringe (2.9 cm needle) fired from a Palmer Cap-Chur[®] rifle (Douglasville, Georgia). 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. In 1996, we used 2 Robinson R-22 (1-passenger) helicopters for capturing moose, that allowed for simultaneous processing and darting of animals. In 1997 we used 1 Robinson R-44 (3-passenger) helicopter for capturing moose.

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 as needed to determine age from cementum annuli (Gasaway *et al.* 1978); and 4) collected 50 cc of

blood from the jugular vein. Matson's Laboratory (Miltown, Montana) processed tooth samples for age determination. R. L. Zarnke (Alaska Department of Fish and Game, Fairbanks) processed blood, and serum was analyzed (Bio Tracking, Moscow, Idaho) for pregnancy-specific protein B (PSPB) (Russell *et al.* 1998). T. R. Stephenson (Alaska Department of Fish and Game, Soldotna) 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) 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 radio-tracked 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 Supercub) 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 from radiocollared females and 18 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 to be 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. Female-offspring pairs often were in clearings that permitted landing within a few meters of the young, and disturbance from the helicopter usually was sufficient to frighten females away from neonates and the capture crew. If the female-offspring pair was not in or near clearings, the capture crew (with radio communication) exited the helicopter in a nearby landing area. The helicopter then hovered above the young in an attempt to frighten the female away. We monitored all captures from fixed-wing aircraft. 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) 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 to be >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) 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 confirmation of rebonding, we listened to signals of young to determine 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. 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 died. No young from the 1997 cohort lost their collars.

Statistical Analyses

Two-tailed *t*-tests using 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. 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 using the Z-test (Remington and Schork 1970:217). Sources of mortality were compared between 1996 and 1997 using 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 Inc., Cary, North Carolina). 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 is superior to nonparametric analysis if assumptions are satisfied (Efron 1988) and parametric methods deal with covariates and interactions better than nonparametric methods such as the Kaplan-Meier method. We assumed a Weibull error distribution for the regression model because it is a flexible proportional-hazards model that naturally scales hazard rates that depend on covariates. We used PROC LIFEREG to build 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.

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 female 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 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

A histogram of adult age structure indicated the moose population was well represented by young and middle-aged females in 1996 (Fig. 1). Because the same moose were sampled in 1997, females were on average 1 year older. Mean age of an adult female was 6.8 yrs ($SD = 3.3$ yrs, $n = 45$) in 1996. The oldest moose was estimated at 13 years of age. In 1996, 98% of 44 adult females were pregnant, and in 1997 the pregnancy rate was 77% of 30 adults; the difference in pregnancy rates 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 ($Z = 2.18$, $P = 0.03$).

Maximum depth of rump fat was 63% lower in 1997 than during 1996 (Table 1). Mean maximum depth of rump fat was significantly greater among pregnant versus nonpregnant females (t -test assuming unequal variances, $t = -4.72$, $df = 12.9$, $P = 0.001$; Table 2). Mean maximum depth of rump fat also was significantly greater for females giving birth to twins versus those with singletons (t -test, $t = -2.88$, $df = 52$, $P = 0.006$;

Table 2). Regression indicated that no relationship existed between rump-fat depth and age for our 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, with 80% of births occurring within 11 days and 95% of births within 14 days. In 1996 the median date of birth was 19 May, and the mode for births occurred on 20 May. 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, and the mode for births occurred on 20 and 21 May. Distributions of births approximated normality and were skewed slightly right (Fig. 2). Timing of parturition for radiocollared females was significantly different in 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. 3) did not differ between years (Smirnov 2-sample test, $P > 0.2$).

Mean birth mass was 13.7 kg ($SD = 1.6$ kg, $n = 15$) for twins and 17.0 kg ($SD = 2.6$ kg, $n = 66$) for singletons. Individual twins weighed significantly less than singletons (males and females pooled, t -test, $t = 4.67$, $df = 79$, $P < 0.0001$) and female singletons weighed significantly less than did their male counterparts (t -test; $t = -2.82$, $df = 61$, $P = 0.007$; Table 3).

Regression analysis indicated a significant ($P = 0.04$) negative relationship (slope = -1.355) between birth date and maximum depth of rump fat in March. For that model

we 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 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*birth mass for twins) was also positively related to rump-fat of females in March ($r^2 = 0.28$, $df = 44$, $P = 0.0002$; Fig. 4).

Mortality

During the first year (1 March 1996 - 28 February 1997), predators killed 7% of 44 radiocollared adult female moose. 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 March 1997 - 28 February 1998), predators killed 5% of 43 adult female moose with radiocollars. 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-induced reasons (trampling by female or abandonment following release), and we eliminated those individuals from the survival analysis. We observed 2 stillbirths (one each in 1996 and 1997), one from a set of twins and one a singleton.

Radiocollared young experienced a high annual rate of survival (53%, Fig. 5) 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. 6). Nonpredation mortality was attributed to drowning, malnutrition, and injuries inflicted by other moose.

In 1996 we did not detect births for 15% of 41 pregnant females, and in 1997 for 13% of 23 pregnant females. These females were previously determined to be pregnant during March based on both transrectal ultrasonography and PSPB analyses in 1996 and PSPB analysis only in 1997. This observation may be accounted for by perinatal mortality (mortality that occurred during the first 24 hours after birth), intrauterine mortality (mortality occurring between the diagnosis of pregnancy in March and the birthing period), or incorrect pregnancy diagnosis.

Relations between Neonate Condition, Female Condition, and Young Mortality

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 using parametric regression provided the following model: $\log(\text{expected time-to-death}) = -4.485 + 0.718\text{birth date} + 1.546\text{litter size} + 0.727\text{birth mass} - 0.049\text{birth mass}*\text{birth date} - 0.017\text{birth mass}*\text{birth date}*\text{litter size}$. Birth year and sex did not enter the model at $P > 0.15$. This model indicated that expected time-to-death 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. 7a), but the differing rate of increase in each category (early born singleton, early born twin, late-born singleton, late-born twin; Fig. 7a) partly explained the 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. 7b).

We also studied the relationship between survival of young to 1 year old and female age, measures of female rump-fat depth, and female 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 with radiocollars in spring 1996 indicated that our study population was well represented by young and middle-aged moose (2 -8 years; Fig. 1), which is 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 is relative to "carrying-capacity" (K), past research suggests that moose in our population are approaching the upper limits of density reported by Gasaway *et al.* (1992).

Physical condition of adult females (Table 1) and their timing of births (Fig. 2) differed between years with similar mild winters. Pregnancy rates of adults (98% in 1996 and 77% in 1997) also differed between the 2 years. Moose populations below K tend to

exhibit high rates of pregnancy and reproduction (Boer 1992, Gasaway *et al.* 1992, Schwartz 1998, Bowyer *et al.* 1998b). Individuals in poorer condition have a decreased probability of becoming pregnant (Heard *et al.* 1997). Twinning rates obtained from the same radiocollared females followed a pattern similar to the overall rate of pregnancy we observed. Twinning differed between years with 31% in 1996 and 10% in 1997. Both pregnancy rate and twinning rate are regarded as indicators of range conditions or productivity in moose populations (Gasaway *et al.* 1992, Bowyer *et al.* 1998b, Schwartz 1998). The differences in pregnancy and twinning we observed between years suggest adult females exhibited variability in their ability to compensate for environmental or reproductive factors, likely as a response to increasing population density (McCullough 1979, Testa 1998). Both the winters of 1996-97 and 1997-98 had relatively low snowfall. Snow has not been reported to significantly restrict travel of moose until depth accumulates to >71 cm (Kelsall 1969, Coady 1974), well above the reported level of snowfall for our study area. That outcome indicates snowfall did not play a major role in the marked variation we observed in indices of productivity for female moose.

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 this previous research, mortality in our study was evenly distributed between black bears, grizzly bears and wolves (Fig. 6), although at a low overall rate (Fig. 5).

We conclude there is a direct link between maternal condition and condition of offspring. We noted the fattest females produced the heaviest newborns (Fig. 4). Additionally, both adult pregnancy and litter size were significantly related to depth of rump-fat in March (Table 2). Female moose giving birth to twins were in better condition than those giving birth to singletons. The correlation between litter size and female condition differ from the findings of Testa and Adams (1998), who reported no link between fat depth and litter size. 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 births 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 whether the condition of young moose at the time of birth would influence their future survival, we tested whether survivorship could be explained, in

part, by birth variables. Previous research in predator-rich environments has shown early survival of northern cervids can be influenced 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 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 using 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 other effects. Decreasing slopes (Fig. 7) indicated that later-born individuals have decreased time-to-death 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. 7) demonstrated that heavier-born young have increased times-to-death 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.

Finally, to test the hypothesis that survival of young was predetermined by female condition, we studied the relationship between survival to 1 year-of-life in young moose and condition indices of adult females. Cameron *et al.* (1993) concluded that young caribou born to females in poorer condition (decreased summer mass) 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. Females 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 using parametric regression indicated that no measures of female condition we collected (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. 4), birth date of offspring, and litter size (Table 2), 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. 7). 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 weight 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 appears to be a direct link to 3 factors that significantly influence survival of young in our study area. That outcome implies survival of young may be predetermined by factors acting upon the female prior to birth. Thus, we hypothesize that some of the mortality in this population was likely compensatory. That conclusion differs from many areas of Alaska, where mortality of young is thought to be largely independent of their physical condition, in particular in areas where predators hold moose at low densities (Gasaway *et al.* 1992, Bowyer *et al.* 1998b). 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 similar condition, which may occur at lower density, may mask relationships that otherwise may be present. We acknowledge that the relatively high density of moose within our study area likely leads to the production of more total young as well as increased variation in condition of individuals.

We can draw several conclusions with regard to the role environmental conditions and predation played in the 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. Our results do provide evidence that moose timed parturition to maximize the use of the growing season (Bowyer *et al.* 1998b). 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. 7). This reduced survival may result from the inability of young to exhibit compensatory growth during their first summer (Keech *et al.* 1999). In the presence of stochastic variability, however, we acknowledge data from more than 2 consecutive years would be desirable to more adequately explore mechanisms underpinning timing and synchrony of parturition. Nonetheless, evidence from our study supports 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 females in 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. 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.

ACKNOWLEDGMENTS

We thank T. A. Boudreau, R. Hunter, D. G. Kelleyhouse, E. A. Lenart, M. E. McNay, T. O. Osborne, D. J. Reed, C. T. Seaton, T. R. Stephenson, K. P. Taylor, K. R. Whitten, and R. L. Zarnke, of the Alaska Department of Fish and Game, and L. K. Duffy and E. B. Finch of the University of Alaska Fairbanks, for their help during this study. We also thank airplane pilot M. Webb and helicopter pilots J. Larrivee, L. Larrivee, D. Sheplar, and R. Swisher. This study was supported by funds from Federal Aid in Wildlife Restoration, Alaska Department of Fish and Game, Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, and Department of Biology and Wildlife, University of Alaska Fairbanks. All aspects of this research were in accordance with acceptable methods for field studies adopted by the American Society of Mammalogists (Animal care and use committee 1998).

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Table 1. Summary statistics for depth of rump fat for adult female moose captured during March 1996 and 1997 in interior Alaska, USA.

Parameter	1996			1997		
	$\bar{x}$	<i>SD</i>	<i>n</i>	$\bar{x}$	<i>SD</i>	<i>n</i>
Adult rump fat						
at midpoint (cm)	0.6*	0.4	42	0.4*	0.4	30
Adult rump fat						
at maximum (cm)	1.6**	1.0	43	1.0**	0.9	30

*Difference significant ($P = 0.05$), t-test; **Difference significant ($P = 0.01$), t-test.

Table 2. 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	Rump fat at midpoint (cm)			Rump fat at maximum (cm)		
	$\bar{x}$	<i>SD</i>	<i>n</i>	$\bar{x}$	<i>SD</i>	<i>n</i>
Nonpregnant						
adult females	0.05*	0.11	8	0.33*	0.57	8
Pregnant adult						
females	0.55*	0.43	64	1.44*	0.99	65
Females						
producing						
singletons	0.51***	0.42	42	1.29**	0.93	42
Females						
producing						
twins	0.81***	0.43	11	2.16**	0.92	12

*Difference significant ($P \leq 0.001$), t-test for unequal variances; **Difference

significant ($P \leq 0.01$), t-test; ***Difference significant ($P \leq 0.05$), t-test.

Table 3. Summary statistics for mass of newborn moose captured during May 1996 and 1997, in interior Alaska, USA.

Year	^c Singleton						^c Twin					
	^b Birth mass ♂ (kg)			^b Birth mass ♀ (kg)			Birth mass ♂ (kg)			Birth mass ♀ (kg)		
	$\bar{x}$	<i>SD</i>	<i>n</i>	$\bar{x}$	<i>SD</i>	<i>n</i>	$\bar{x}$	<i>SD</i>	<i>n</i>	$\bar{x}$	<i>SD</i>	<i>N</i>
1996 ^a	18.9	3.0	10	16.4	2.6	17	14.1	2.4	4	13.5	1.4	6
1997 ^a	17.6	2.2	15	16.2	2.3	21				14.4	1.1	3
Pooled												
(96-97)	18.1	2.7	25	16.3	2.4	38	14.1	2.4	4	13.8	1.3	9

^aNo significant difference between years ($P > 0.2$) within sex or sibling status groups, t-

test; ^bMean birth mass for male versus female singletons was significantly different in

1996 ($P = 0.04$), 1997 ($P = 0.08$), and combined 96-97 ($P = 0.01$), t-test; ^cMean birth

mass of singleton and twin males was significantly different in 1996 and combined 96-

97 ($P = 0.02$ and 0.01 , respectively). Mean birth mass of singleton and twin females

was significantly different in 1996 and combined 96-97 ($P = 0.02$ and 0.005 ,

respectively), difference not significant in 1997 ($P = 0.21$), t-test.

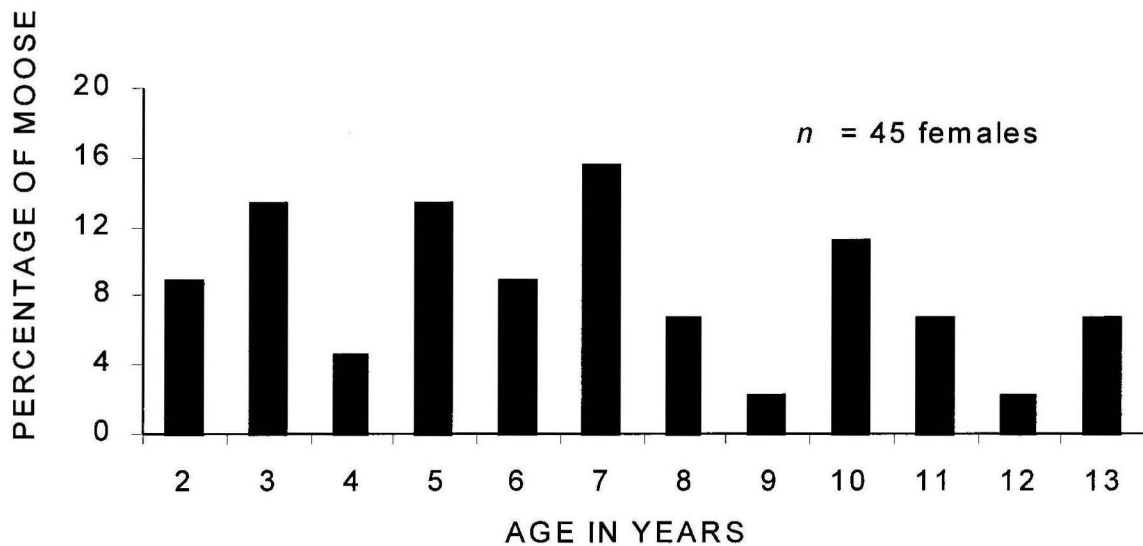


Fig. 1. Distribution of ages for radiocollared adult female moose in interior Alaska, USA, during 1996. Moose from this sample were used to determine pregnancy rate, twinning rate, parturition date, and rump-fat reserves during 1996 ($n = 44$) and 1997 ($n = 30$). These females were also monitored for mortality rate and their young were captured following parturition.

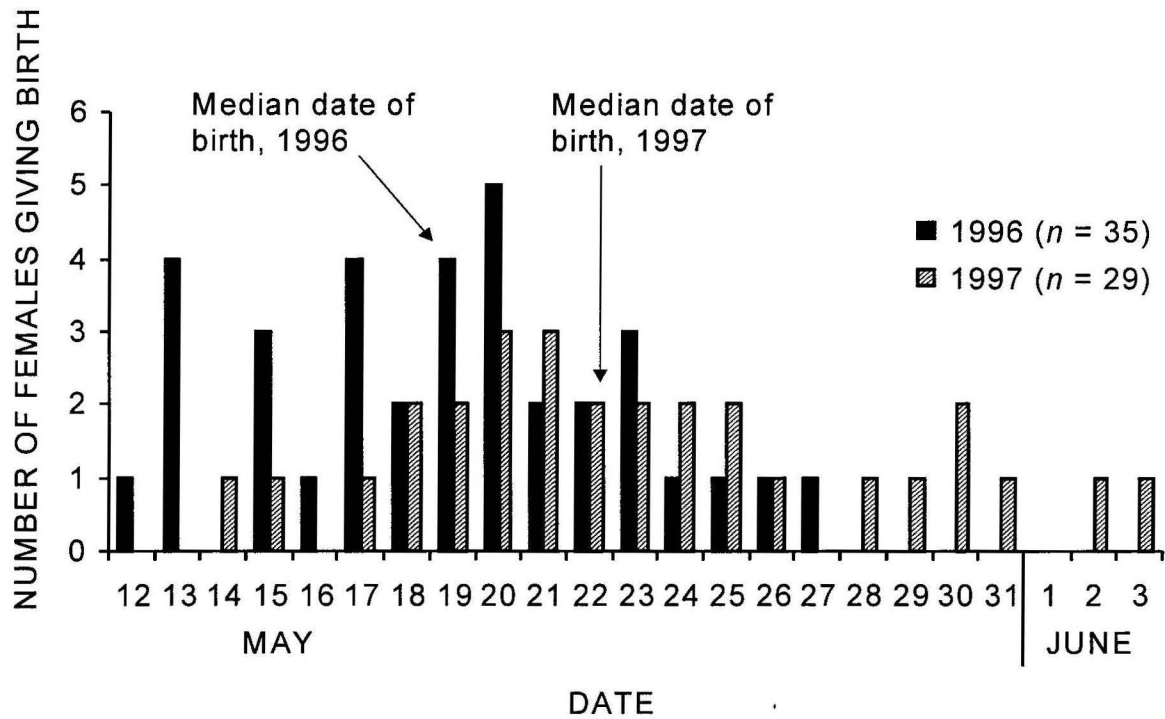


Fig. 2. Timing and date of parturition for female moose in interior Alaska, USA, during 1996 and 1997.

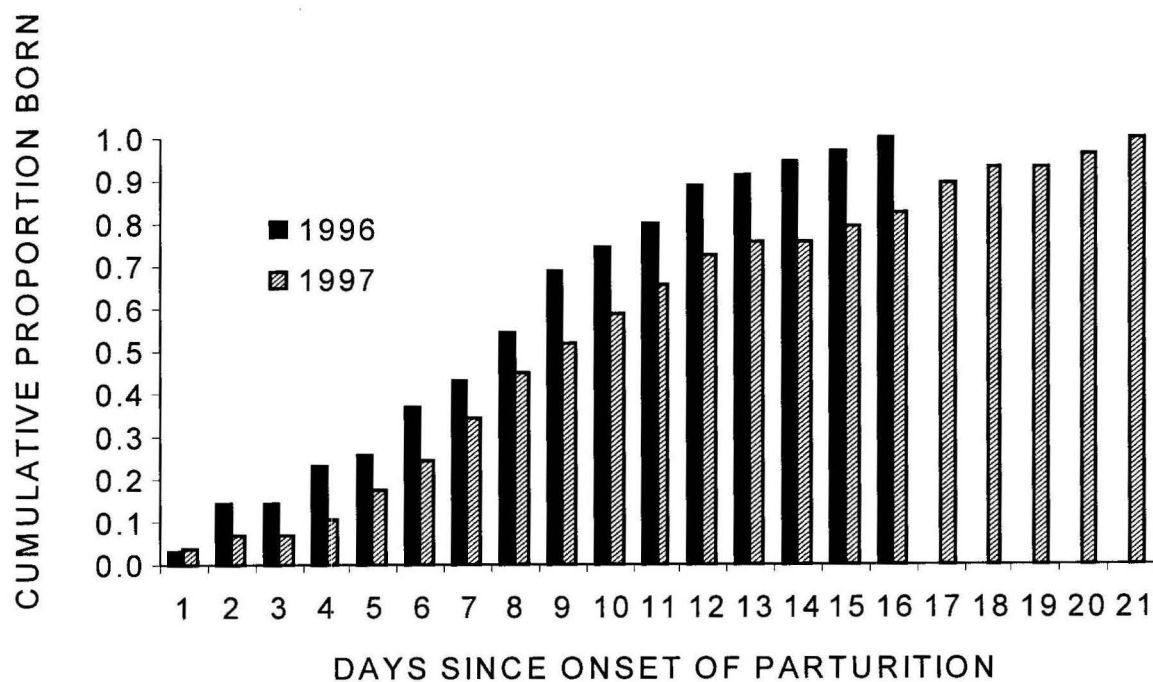


Fig. 3. Cumulative proportion of moose young born to radiocollared females, based on days since onset of parturition, during 1996 ($n = 35$) and 1997 ($n = 29$) in interior Alaska, USA.

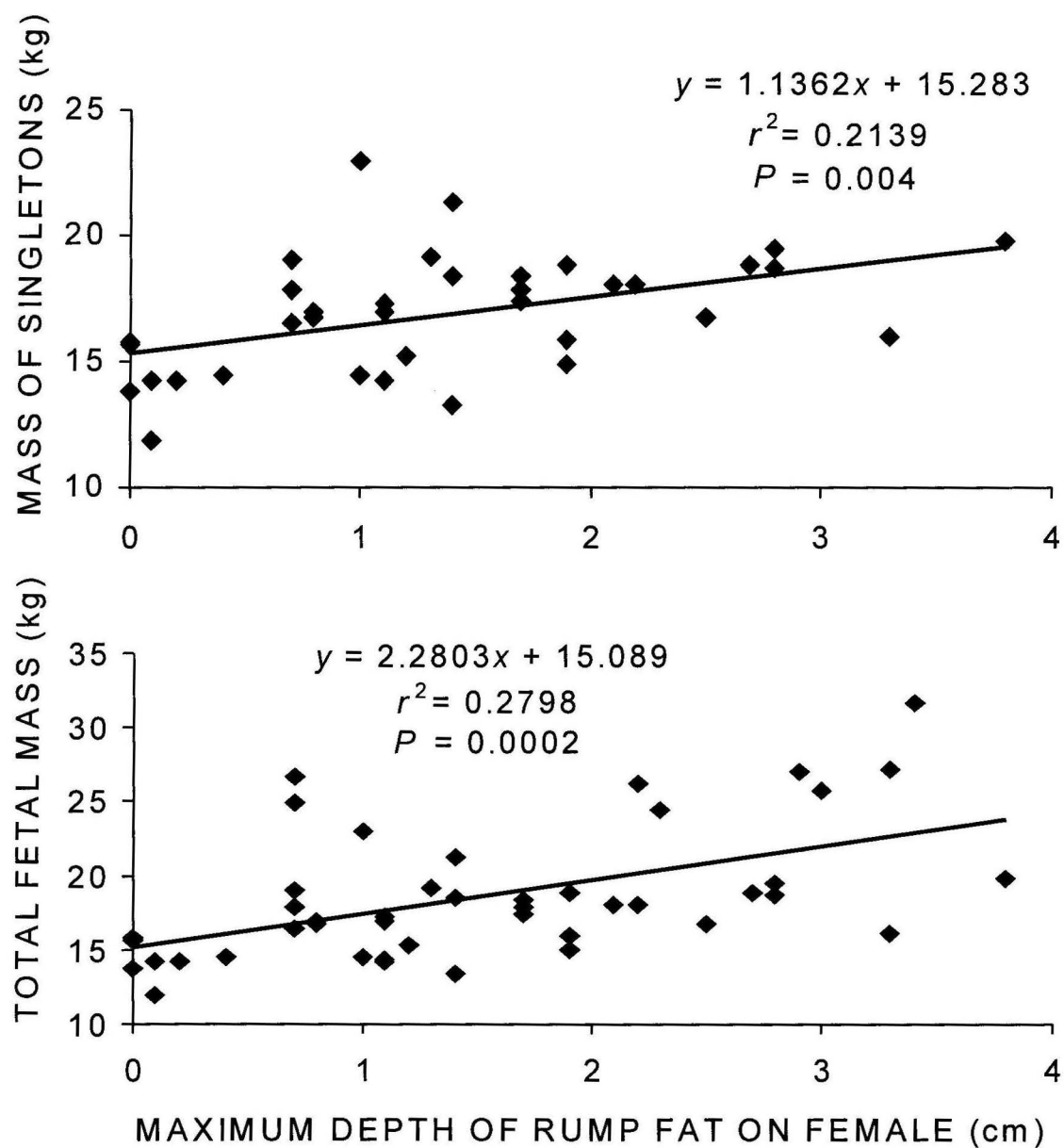


Fig. 4. Relationship between depth of rump fat in March and birth mass of singleton newborns ($n = 37$), and between depth of rump fat in March and total fetal mass ($n = 45$). Moose from interior Alaska, USA, 1996 and 1997.

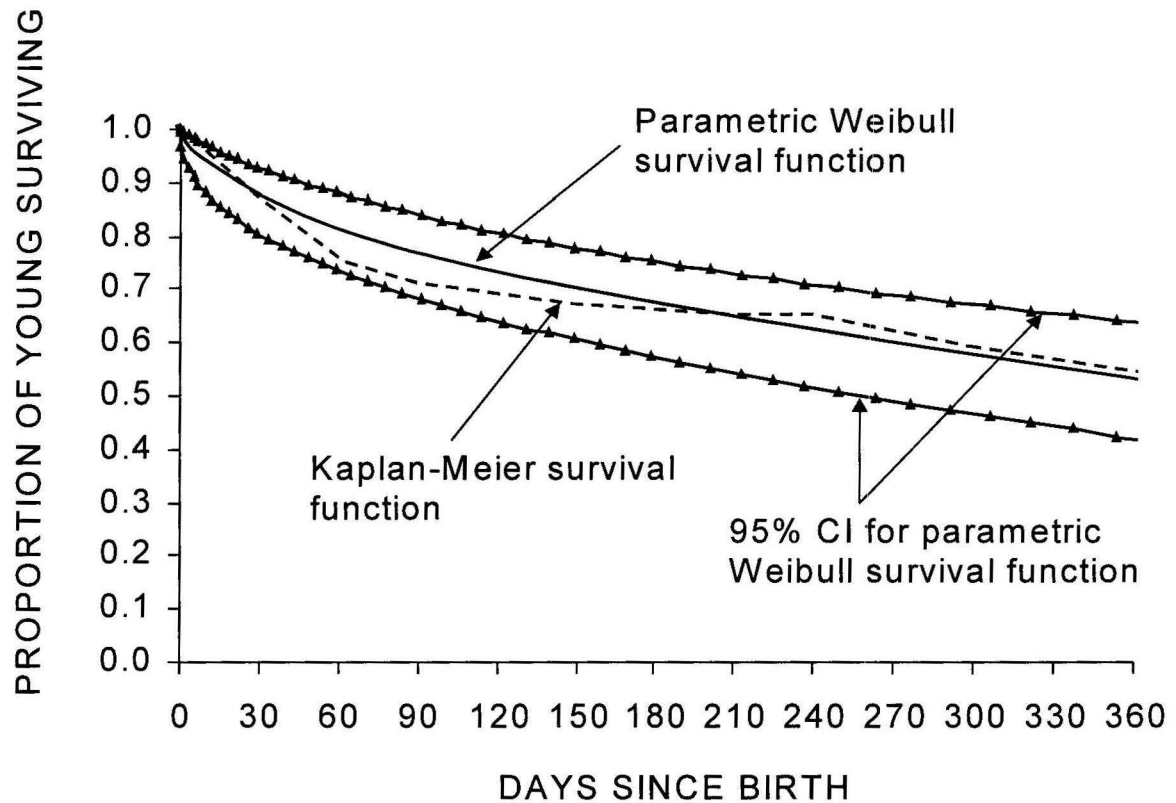


Fig. 5. Parametric survival curve (error distribution = Weibull) for young moose from birth to 365 days-of-life in interior Alaska, USA, 1996 and 1997 ($n = 81$).

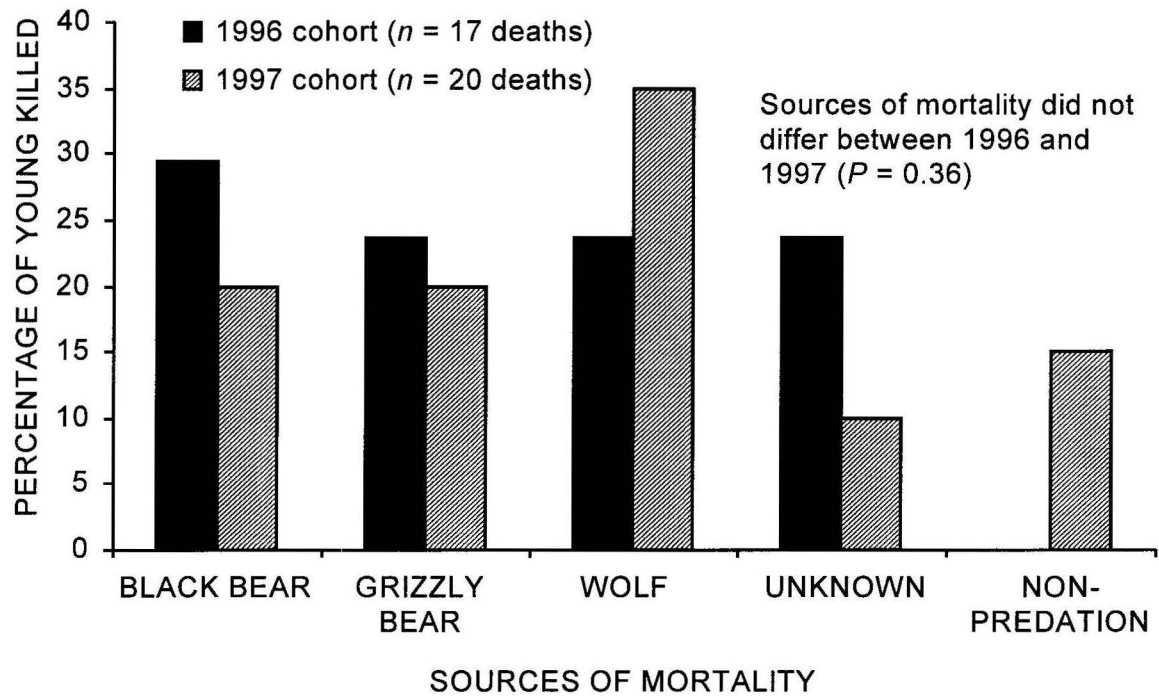


Fig. 6. Distribution of mortality sources for young radiocollared moose that died during 1996 and 1997 in interior Alaska, USA.

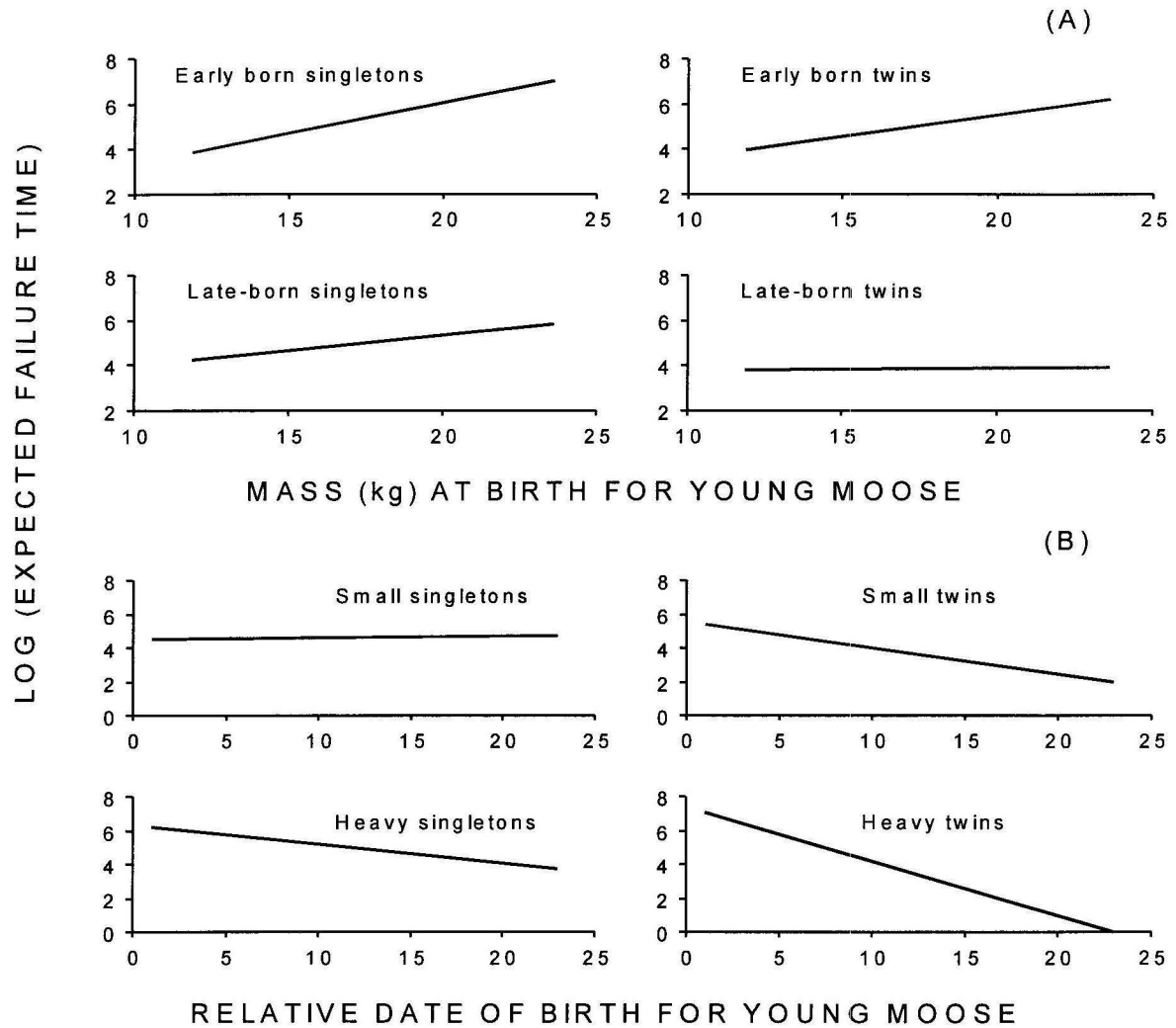


Fig. 7. Relationship between birth date, birth mass, litter size, and log of expected failure time (death), for 81 moose captured as newborns in interior Alaska, USA, during May 1996 and 1997. Categories for young include; small born (mass at birth = 14.5 kg), heavy born (mass at birth = 18.1 kg), early 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).