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TIMING AND SYNCHRONY OF PARTURITION IN ALASKAN MOOSE: LONG-TERM VERSUS PROXIMAL EFFECTS OF CLIMATE

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We studied timing and synchrony of parturition in Alaskan moose (*Alces alces*) in Denali National Park and Preserve, Alaska, from 1990 to 1994. Mean date of birth was 25 May ($SD = 5.7$ days) and did not differ significantly among years. Although moose did not congregate to give birth, parturition was highly synchronized (95% of births occurred in 16 days) with no significant differences among years. Most young moose were killed by predators, especially grizzly bears (*Ursus arctos*), but timing of reproduction had no effect on survivorship of young, which was low (ca. 0.2 by 16 June). We reject the hypothesis that moose timed births to avoid predation. We also measured depth of snow in winter, and precipitation, cloud cover, and temperature in spring; none of these variables was related to timing or synchrony of births. Likewise, quality of willow (*Salix pulchra*) in 3 springs in which percent nitrogen and in vitro dry-matter digestibility of this important forage varied markedly was unrelated to timing of births. We reject the hypothesis that moose timed parturition in response to proximal changes in their environment. We hypothesize that both timing and synchrony of parturition in moose are adaptations to long-term patterns of climate that provide the most hospitable conditions to bear and rear young. Consequently, moose may be more susceptible to climatic change than other ungulates that are more adapted to climatic variability.

Key words: *Alces alces*, moose, parturition, synchrony, predation, survivorship, weather, forage, climatic change, Alaska

Why mammals living in temperate and arctic environments breed synchronously and the environmental factors affecting timing of births have been topics of considerable interest and debate (Bronson, 1989; Ims, 1990; Millar, 1977). This phenomenon has been especially well studied among ungulates with detailed research on white-tailed deer (*Odocoileus virginianus*—Kie and White, 1985; McGinnis and Downing, 1977; Ranson, 1966; Verme and Ozoga, 1987; Weber, 1966), mule deer (*O. hemionus*—Bischoff, 1957; Bowyer, 1991; Robi- nette et al., 1977), red deer (*Cervus elaphus*—Clutton-Brock et al., 1987; Guinness et al., 1978; Iason and Guinness, 1985),

bighorn sheep (*Ovis canadensis*—Festa-Bianchet, 1988; Thompson and Turner, 1982), Dall's sheep (*O. dalli*—Bunnell, 1980; Rachlow and Bowyer, 1991), and bison (*Bison bison*—Berger, 1992; Rutberg, 1984).

Although timing of births in northern ungulates is entrained by photoperiod (Budde, 1983; Verme and Ozoga, 1987), substantial variation in dates of birth around this environmental cue are evident. For instance, Bowyer (1991) reported a 2-month difference in peak births for populations of mule deer in coastal and montane areas of southern California at similar latitudes. These populations timed parturition differently so

that nutritional needs of female deer for reproduction could be met (Bowyer, 1991). Altitudinal variation in timing of births also has been reported for white-tailed deer (Ransom, 1966). Thus, photoperiod is an important cue to help time reproduction but cannot explain why mammals give birth at a particular time or why they do so synchronously. Two prevailing hypotheses have been advanced to explain timing and synchrony of parturition for large herbivores: 1) climatic effects on animals or on seasonal patterns of forage availability and quality; and 2) predation (Bunnell, 1982; Rutberg, 1987).

Climate may influence reproduction in several ways. First, severe weather may directly affect neonates via hypothermia or reduce energetic reserves of parturient females coping with deep snow (Rachlow and Bowyer, 1991). Second, weather may affect quality and abundance of forage during critical periods and thereby influence timing of reproduction. Late-born young may be underweight and suffer higher rates of mortality than those born earlier (Clutton-Brock et al., 1987). Moreover, females on a low nutritional plane in winter (Langenau and Lerg, 1976) or experiencing delayed green-up of forage in spring (Rachlow and Bowyer, 1994) may reduce maternal investment in their young. Clearly, females must have sufficient energy and nutrients to meet high costs of lactation (White and Luick, 1984). Additionally, the short growing season in northern environments may promote synchronous births in early spring to allow time to provision young successfully (Bunnell, 1982; Festa-Bianchet, 1988; Rachlow and Bowyer, 1991).

Estes (1976) and Estes and Estes (1979) proposed that synchronous births would swamp predators with more young than they could kill and consume, thereby lowering risk of predation for individuals, in contrast to a strategy of spreading births more evenly through time. Species that congregate during or after parturition also may

gain additional benefits relative to predation from group living (*sensu* Hamilton, 1971).

Alaskan moose (*Alces alces*) inhabit a predator-rich environment with a severe and highly variable climate (Gasaway et al., 1992; Miquelle et al., 1992; Molvar and Bowyer, 1994). Thus, moose offer a unique opportunity to explore factors that underpin timing of reproduction. We quantified timing and synchrony of births for one population of Alaskan moose over 5 years and tested effects of predation, weather, and quality of forage on patterns of reproduction. We also discuss the potential role of climatic change on populations of moose.

MATERIALS AND METHODS

Study area.—We conducted this study in the eastern portion of Denali National Park and Preserve (63°45'N, 149°50'W) in interior Alaska during 1990–1994. Our study area extended from the Park entrance to the Sanctuary River and encompassed ca. 300 km². Moose generally occurred at elevations ranging from 700 to 1,200 m in a broad valley, enclosed by rugged foothills to the north and steep terrain of the Alaska Range to the south (Miquelle et al., 1992). About 150 moose were present during the course of our study; 11–18 adult females were fitted with radiocollars each year through our 5-year study. The vegetation was a mosaic of open stands of spruce (*Picea glauca* and *P. mariana*) and willow (*Salix*) understory, interspersed with brushy tundra dominated by resin birch (*Betula glandulosa*). Alpine tundra occurred at higher elevations, and riparian zones followed numerous meandering rivers, creeks, and intermittent washes (Molvar et al., 1993).

The Park possessed a full complement of large mammalian predators, and wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) occurred at relatively high densities for those carnivores (Albert and Bowyer, 1991; Miquelle et al., 1992). This population of moose was typical of many populations in interior Alaska that were held at low density by predation (Gasaway et al., 1992; Van Ballenberghe and Ballard, 1994).

Sampling procedures.—We determined dates of birth for moose by tracking adult females wearing collars with radiotransmitters and searching for neonates while driving along the Park Road. We typically radiotracked females

each morning and evening from early May through mid-June 1990–1994 to determine their location and if they had given birth; that period encompassed both the peak of births and >1 week both before and after the first and last births occurred. When a radio signal indicated a female had remained stationary for several sequential fixes, we followed the signal to the location of that female. Females with neonates tend to remain at or near the site of birth for 1–3 weeks following parturition, if they are not disturbed by people or predators. We took great care not to alarm females or young. We recorded the number of young, their location, and estimated their age. We did not estimate date of birth of young >4 days old. If a radiocollared female was not observed with young following the birthing season, she was eliminated from our analysis during that year; we could not be certain if such females failed to give birth or had already lost young to predators or other causes when we first observed them.

We continued monitoring females with young to determine their survivorship through mid-June and again during September, but we seldom approached them closely until they had moved from the site of birth. We returned to the site of birth, however, if we suspected that either the female or her offspring had been killed by a predator. We determined which predator was responsible by directly observing bears or wolves at or near the site of a recent kill or actually making a kill, or more rarely by examining the site for signs of the predator. Care was taken in making the latter determination because we have observed bears and wolves scavenging kills from each other.

We also searched for newborn moose each morning and evening by driving west and returning east along the Park Road, surveying areas on both sides, for a total of ca. 80 km (40 km each way). We used one vehicle in 1990–1991 and searched independently using two vehicles in 1992–1994. In 1993, we also searched for neonates from a small fixed-winged aircraft for ca. 3 h on 1 day.

We clipped stems and leaves of diamond leaf willow (*Salix pulchra*), a common forage of moose (Van Ballenberghe et al., 1989), from three sites in our study area at weekly intervals from mid-May to mid-June 1992–1994. One site was near Park Headquarters (ca. 3.2 km W of the Park entrance), the second was ca. 19 km W

along the Park Road, and the third was near Hogan Creek (ca. 35 km W along the Park Road). Elevation of these sites ranged from ca. 730 to 915 m. At each site we clipped twigs of current annual growth at the most recent bud-scale scar from each of ca. 15 willows. That sample included new growth of stems, leaves, and catkins—the plant parts we observed moose eating at that time of year. We dried (50°C) and ground the sample so it would pass a 1-mm screen, and nitrogen (micro-Kjeldahl) and in vitro dry-matter digestibility (using rumen liquor from a caribou, *Rangifer tarandus*, fed a diet with willow) were determined using standard techniques (Van Soest, 1982) at the University of Alaska Fairbanks.

We obtained climatic data from the Alaska State Climate Center in Anchorage, Alaska, and from files at Denali National Park and Preserve. The McKinley Park Weather Station (elevation 730 m) was located near Park Headquarters in the eastern one-third of our study area. We analyzed data on mean depth of snow from November to April. Depth of snow would be expected to affect energy balance of pregnant females (sensu Mautz, 1978) and thereby timing and synchrony of parturition. Likewise, we examined ambient temperature, precipitation, and percentage of days that were cloudy or overcast during May and June—the period during which those variables should influence growth of plants. We also calculated number of degree-days >5°C (the number of degrees that the mean daily temperature was >5°C, summed across all days). This variable was selected because it provided an index of growth for plants in arctic environments (Chapin, 1983).

Statistical analyses.—We tested for differences among median dates of birth and in litter size among years using the *G*-test (Zar, 1984). We compared slopes of regression lines using the *F*-test and used the Spearman rank correlation to test for effects of weather variables on timing and synchrony of births. We estimated survivorship of young moose using the Kaplan-Meier procedure with staggered entry of animals into the study (i.e., births) and with right censoring of young when their survival time was known only to be greater than some value (Pollock et al., 1989). We compared survival curves of young moose using the log-rank test modified for staggered entry of animals (Pollock et al., 1989). The null hypothesis was that survival

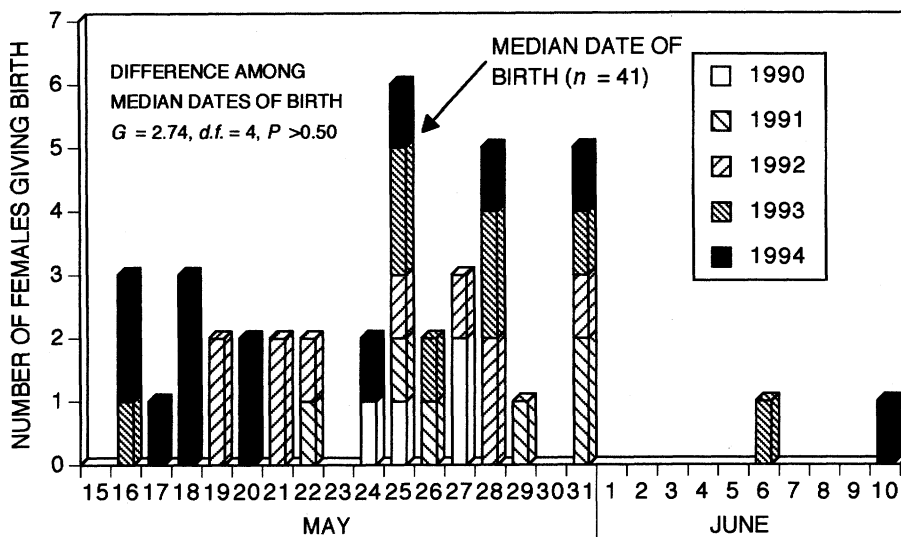


FIG. 1.—Timing of parturition for female Alaskan moose in Denali National Park, Alaska, 1990–1994.

functions came from the same underlying curve. We also calculated 95% confidence intervals for estimates of survivorship according to Pollock et al. (1989).

RESULTS

Births were about equally divided between singletons ($n = 24$) and twins (22) from 1990 to 1994; we observed only one set of triplets. No significant difference existed among years in number of females giving birth to one versus two or three young ($G = 2.15$, $d.f. = 4$, $P = 0.5$). One female that was radiocollared for all 5 years, gave birth to one, one, two, two, and one offspring, respectively; no other female was radiomonitored for >3 consecutive years. Proportion of births that were twins and triplets ranged from 0.32 to 0.64 during the 5-year study.

Median dates of birth from 1990 to 1994 were 26 May, 27.5 May, 23 May, 27 May, and 20 May, respectively. Timing of births did not differ significantly during the 5-year study (Fig. 1). Distribution of births was only slightly skewed right; median, mode, and mean ($SD = 5.7$ days) were identical with years pooled (25 May, Fig. 1). Females giving birth to two or more offspring,

however, did so earlier (24 May) than those delivering a single young (27 May; test for difference between medians, $G = 6.96$, $d.f. = 1$, $P < 0.01$).

Synchrony of births did not vary among years; no significant difference existed in slopes of regression lines relating cumulative percentage of births and days from onset of parturition (Fig. 2). With years pooled, 80% of births occurred over 11 days, and 95% of births in 16 days.

Causes of death for young moose were attributable mostly to predators. Of 32 young for which we estimated date of death from 1990 to 1994 (i.e., there was evidence of a kill or carcass, or they were never again observed with their mother), 40.6% perished from undetermined causes, 31.3% were killed by grizzly bears, an additional 21.9% were likely killed by bears, and 6.2% were killed or likely killed by wolves (one in each category). Of young moose for which we could determine or infer cause of death ($n = 20$), only the death of one animal was unrelated to predation.

Because we failed to detect significant differences in timing or synchrony of parturition among years (Figs. 1 and 2), we

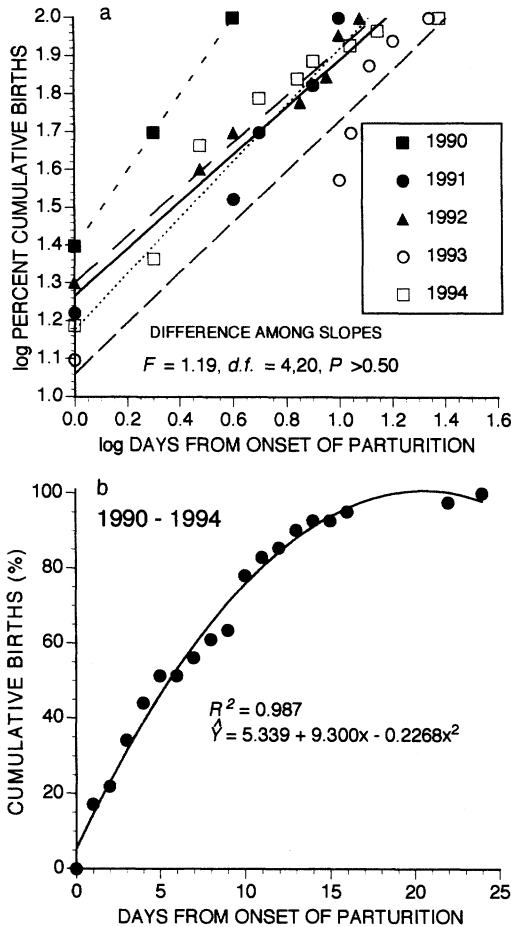


FIG. 2.—Synchrony of births of Alaskan moose by a) year and b) combined in Denali National Park, Alaska, 1990–1994. Regressions equations for individual years were: 1990, $Y = 1.3979 + 1.0002X$; 1991, $Y = 1.1780 + 0.7411X$; 1992, $Y = 1.1300 + 0.6272X$; 1993, $Y = 1.0628 + 0.6678X$; 1994, $Y = 1.2662 + 0.6223X$. Steeper regression slopes indicate greater synchrony of births.

pooled data from 1990 to 1994 to estimate survival of young moose. Survivorship of young declined precipitously over their first month of life; we estimated this parameter was ca. 0.2 by 16 June (Fig. 3). Even the upper bound of the 95% CI for this date was only 0.5 (Fig. 3), and this value was likely biased high because of the small sample caused by the high rate of mortality. Of 44 young born to radiocollared females,

only five (0.11) survived until 1 September—one each from three sets of twins and two singletons.

Young in litters of two or three typically were not killed at the same time by predators; only five of 23 sets of twins and triplets perished together. One adult female also was killed by a grizzly bear while attempting to defend her young. Survival of twins and triplets was not significantly different from singletons (Fig. 3); although twins and triplets were born before single young, it did not affect their survivorship.

To further examine if predation selected for variation in timing of births, we tested for differences in survivorship between young born prior to the median date of birth (25 May) and those born later (young born on 25 May were divided equally between these two periods). No significant difference occurred between young born earlier or later in spring (Fig. 3). Similarly, there was no difference in survivorship of young born at the peak of parturition and in the tails of the distribution (Fig. 3).

Climatic conditions over the 5 years were highly variable. Although depth of snow was greater than the long-term mean during each winter, 1991–1992 was a winter of unusually harsh conditions and deep snow (Fig. 4). Snow persisted into early June and some females delivered neonates onto snow-covered ground in that spring. Likewise, precipitation, percentage of cloudy days, and temperature varied markedly across the 5 years (Fig. 4). Both 1991 and 1993 had below average precipitation during the early growing season (May and June), and unusually warm temperatures in 1993 produced an exceptionally early spring.

No relationship existed between median date of birth and depth of snow (Fig. 4) during our study ($r_s = 0.03$, $P > 0.5$). Similarly, depth of snow was not correlated with synchrony of births (i.e., slopes of regression lines—Fig. 2) over 5 years ($r_s = 0.30$, $P > 0.5$). Surprisingly, depth of snow (Fig. 4) was unrelated to the proportion of

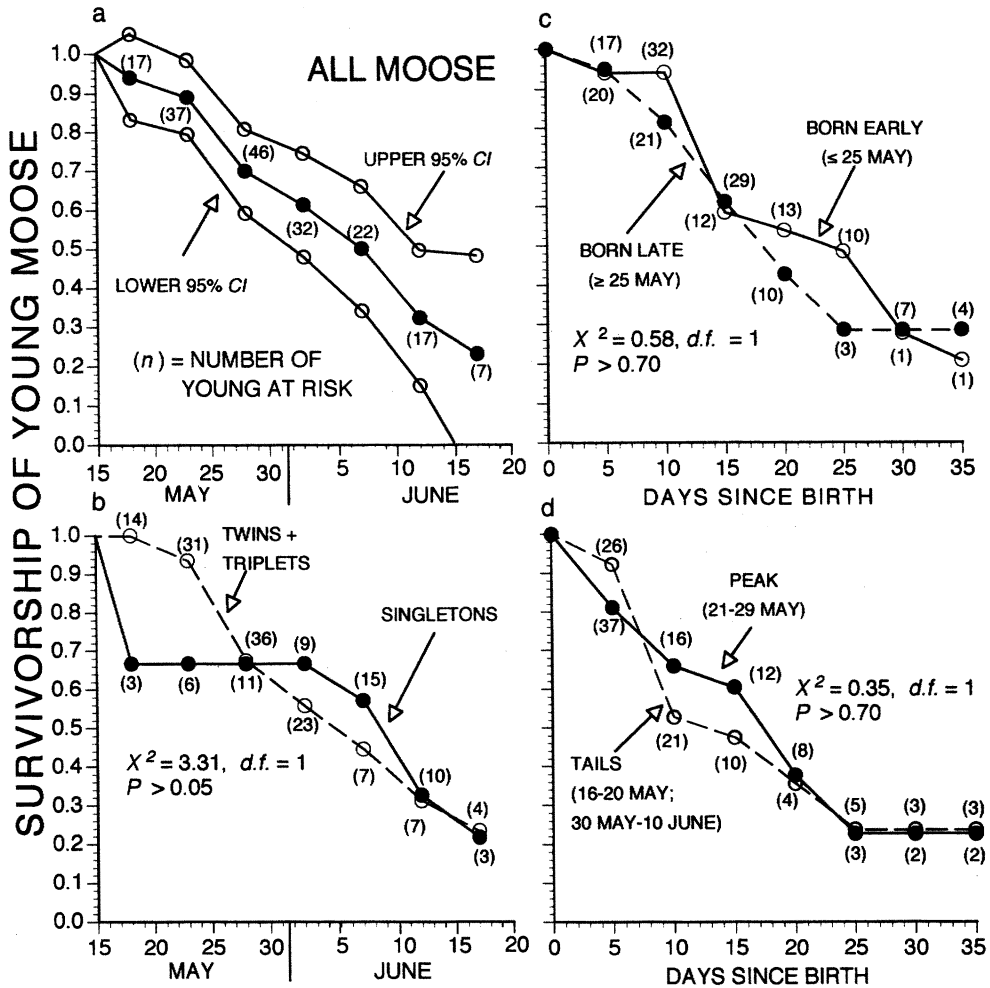


FIG. 3.—Estimates of survivorship by 5-day intervals of young Alaskan moose in Denali National Park, Alaska, 1990–1994. a) Confidence intervals, b) difference in survival between singletons, and twins and triplets, c) differences in survival of young born before and after the median date of birth (25 May), and d) between the peak of births and the tails of the distribution. All parameters are estimated with years pooled. Sample sizes are in parentheses.

twins and triplets produced during each year ($r_s = 0.02$, $P > 0.5$). Indeed, twins composed over one-half of births following the severe winter of 1991–1992 (Fig. 4).

Climatic factors during the early growing season (May–June) were likewise unrelated to median date of birth (precipitation, $r_s = -0.80$; cloudy days, $r_s = -0.41$; temperature, $r_s = 0.20$; $P > 0.2$ for all correlations). No relationship existed between synchrony of births (slopes of regressions in Fig. 2) and weather during early spring (precipita-

tion, $r_s = -0.30$; cloudy days, $r_s = -0.67$; temperature, $r_s = 0.23$; $P > 0.5$ for all correlations).

Weather caused a late spring in 1992, an early spring in 1993, and more typical conditions in spring 1994 (Fig. 4). That climatic variability had a marked effect on early growth and phenology of willows, and thereby quality of forage available to moose near their time of parturition (Fig. 5). Because of extreme climatic differences between the late spring of 1992 and the ear-

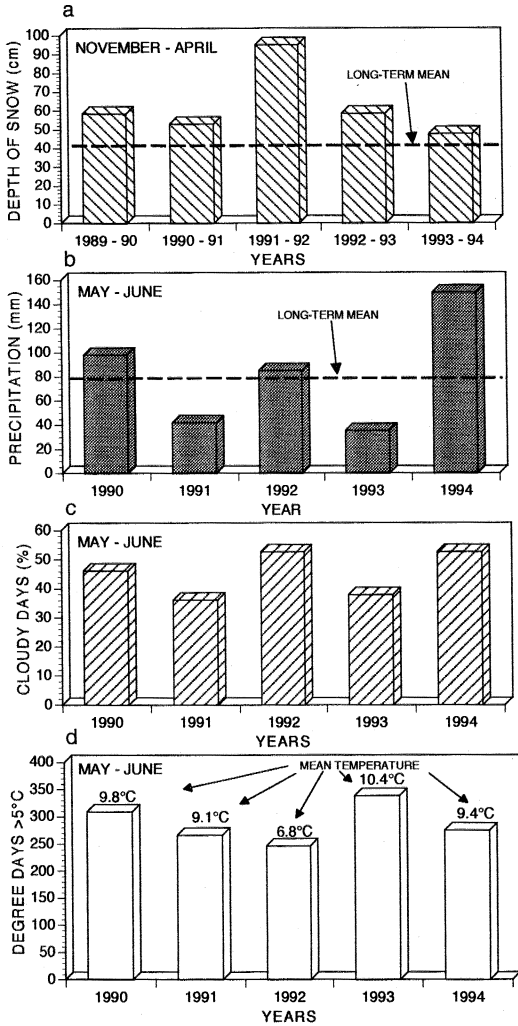


FIG. 4.—a) Mean depth of snow, b) total precipitation, c) percent cloudy or overcast days, and d) cumulative degree days >5°C for the McKinley Park Weather Station, Denali National Park, Alaska, for selected months. Long-term means are from winter 1949 to spring 1994.

ly one in 1993 (Fig. 4), values for quality of forage (Fig. 5) probably represented extremes in variability of in vitro dry-matter digestibility and nitrogen content of forage that moose might encounter during spring. Quality of forage during the late spring of 1992 did not reach its highest level until 9–10 June, whereas in the warm, dry spring of 1993, quality was declining by that date.

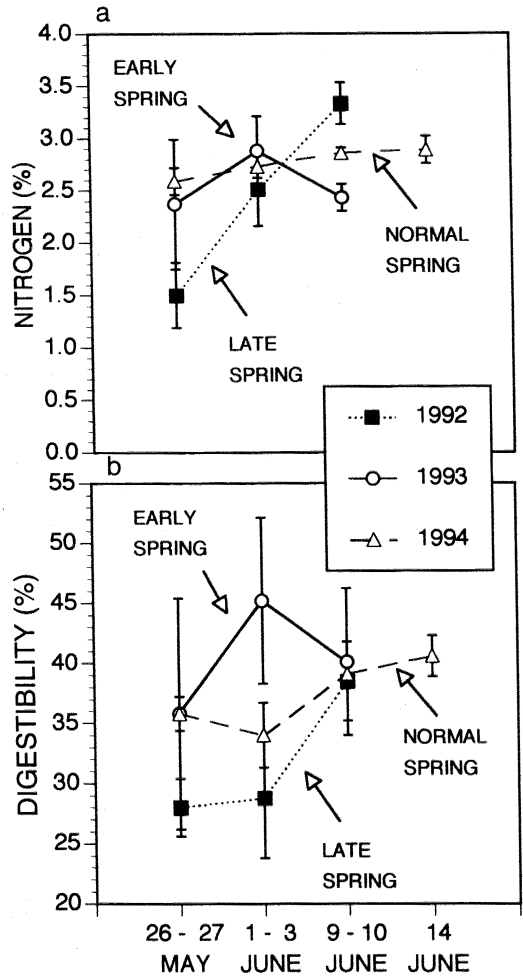


FIG. 5.—a) Mean (\pm SD) nitrogen and b) in vitro dry-matter digestibility for stems and leaves of diamond leaf willow from Denali National Park, Alaska, during spring 1992–1994.

Moose giving birth on or before the median date of birth (Fig. 2) typically would experience relatively poor quality of forage for 1–3 weeks, except during unusually early springs (Fig. 5). Timing and synchrony of births, however, did not vary during our study (Figs. 1 and 2).

The growing season in the Park is highly restricted, with substantial snow accumulating from November to April (Fig. 6). On a long-term basis, the mean maximum temperature does not exceed freezing until mid-April (1°C), and the minimum temperature

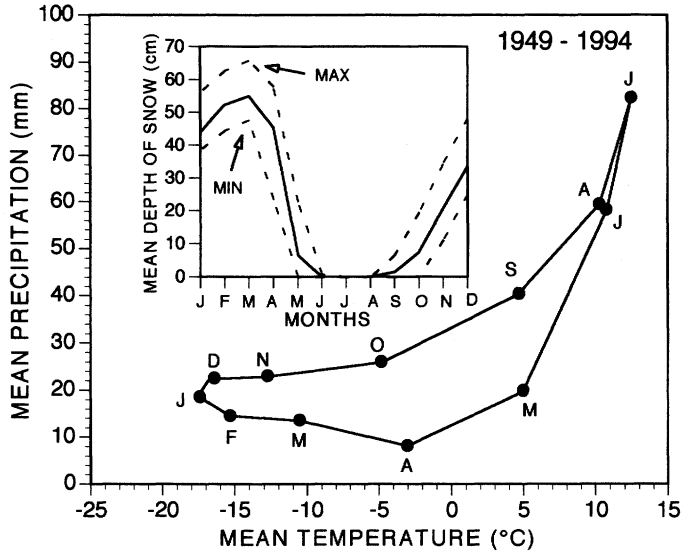


FIG. 6.—Long-term patterns of climate for Denali National Park, Alaska, measured at the McKinley Park Weather Station (730 m elevation). Letters correspond with months.

remains below freezing until late May (0.5°C); likewise, the average daily temperature does not exceed 5°C until May (Fig. 6). The mean minimum temperature for September is below freezing (-3.7°C), and the daily maximum temperature is below freezing by November (-5°C). Although average daily temperature was $>5^{\circ}\text{C}$ until September (Fig. 6), frosts in middle-to-late August caused willows to lose their leaves during 4 years of our study.

DISCUSSION

Moose exhibited consistent timing (Fig. 1) and extreme synchrony (Fig. 2) of births through the 5 years of our study—80% of births occurred in 11 days. Moose neither congregated to give birth (Miquelle et al., 1992) nor occurred in large social groups in spring (Molvar and Bowyer, 1994), yet parturition was more synchronous than for Dall's sheep (Rachlow and Bowyer, 1991), or caribou (Adams and Dale, 1998), which congregate for birthing. Clearly, large congregations of parturient females are not a prerequisite for synchronous births in moose.

Estes and Estes (1979) postulated that

synchronous births served to reduce risk of predation by swamping predators with more young than they could kill during the critical period when neonates were most vulnerable. We observed no evidence that timing or synchrony of births affected survivorship of young moose. Young born earlier did not differ from those born later in survivorship; likewise, young born at the peak of the birthing period did not differ in survivorship from those born earlier or later (Fig. 3). Perhaps young moose benefited from synchronized births after the narrow window in which we measured survivorship. We believe this is unlikely, however, because survivorship of neonates was so low in their first month of life that there would not be sufficient numbers to swamp predators later. Although predators killed most young moose in our study, we reject the hypothesis that the pattern of births was an adaptation to avoid predation. For this pattern to be adaptive, some benefit in survivorship must occur for young born at one particular time over another; this did not occur (Fig. 3). Moreover, the predation hypothesis may explain synchrony in births but not their timing. Thus, some factor oth-

er than predation must be responsible for the consistent timing of births among years (Fig. 1). Rachlow and Bowyer (1991) reached a similar conclusion for the timing of parturition in Dall's sheep.

Moose exhibited small but significant variation in timing of rut among years (Van Ballenberghe and Miquelle, 1993), and perhaps timing of births was simply an outcome of when mating occurred. Indeed, scent-marking by males during rut may help synchronize estrus in female moose (Bowyer et al., 1994; Miquelle, 1991). Nonetheless, there is increasing evidence that female ungulates may alter length of gestation to avoid severe climatic conditions (Rachlow and Bowyer, 1991) or to synchronize parturition (Berger, 1992). Moose conceiving in their second estrus shortened their gestation period and gave birth toward the end of the birthing period of females that conceived in their first estrus (Schwartz and Hundertmark, 1993), and moose in poorer physical condition had longer periods of gestation than females in good condition (Saether et al., 1996; Schwartz and Hundertmark, 1993). Presence of a rutting male may help synchronize estrus in female ungulates (Coblentz, 1976), but needs of the female ultimately determine timing of both mating and birthing (Bowyer, 1991). Timing of rut or a fixed period of gestation were not likely primary reasons for the pattern of births that we observed in moose.

Climate may affect moose directly through such variables as depth of snow and temperature, or indirectly via their influence on the phenology and quality of forage—both hold the potential to determine timing of births. Depth of snow through winter (Fig. 4) may affect energy balance of moose (Coady, 1974), and persistence of snow on the ground the following spring may adversely affect neonates. Winter temperatures are not likely as important; the lower limit of the thermoneutral zone for moose is $< -30^{\circ}\text{C}$ (Renecker and Hudson, 1990). Spring temperatures and precipita-

tion, however, probably affect timing of availability and quality of forage for moose. Indeed, quality of diamond leaf willow, an important forage for moose (Molvar et al., 1993; Van Ballenberghe et al., 1989), varied markedly across 3 springs that were exceptionally variable (Fig. 5). Likewise, cloud cover also would be expected to cause variation in quality of forage for moose among years (Hjeliord et al., 1990). Forage growing in the shade is generally of higher quality than shrubs growing in direct sunlight (Hjeliord et al., 1990; Molvar et al., 1993). Despite extreme variation in weather among years, no significant correlation occurred for timing or synchrony of parturition and any weather variable we measured. Admittedly, the statistical power of these correlations was low because we had only 5 years of data. Nevertheless, inspecting these correlations offered no clear patterns that explained timing or synchrony of parturition in moose. We demonstrated that climate and quality of forage varied among years but reject the hypothesis that moose altered timing or synchrony of parturition with respect to such proximal changes.

Moose that we studied likely were not affected by an extreme climate because they were in excellent physical condition, as evidenced from their high rate of twinning (Franzmann and Schwartz, 1985) in Denali National Park (32–64%). Moose in interior Alaska often are held at densities well below carrying capacity by predation (Gasaway et al., 1992); this also occurred in Denali National Park (Miquelle et al., 1992; Molvar et al., 1993). Because of low survivorship of young (Fig. 3), females seldom undergo the costly process of lactation (White and Luick, 1984) and likely enter winter in excellent condition. Whether moose in poorer physical condition would have shown greater variability in timing or synchrony of parturition is uncertain and deserves further study. White-tailed deer at high population density give birth later and less synchronously than ones at lower den-

sity (Kie and White, 1985; McCullough, 1979), and captive moose fed a diet that resulted in poor nutrition extend the length of gestation (Schwartz and Hundertmark, 1993). Moose also may be buffered against proximal changes in weather because of their large body size (Franzmann, 1981). Newborn moose are quite large (ca. 15 kg) and, therefore, less likely to suffer from hypothermia than smaller-bodied ungulates. Dall's sheep in Denali National Park, only about one-sixth the body mass of moose, exhibited extreme variation in timing of parturition between years with markedly different weather in spring (Rachlow and Bowyer, 1991).

Another hypothesis that would explain low variability in timing of births among years is timing parturition to coincide with long-term patterns of weather that would offer a hospitable environment for bearing and rearing young. Indeed, the 50-year record of weather for the Park indicates that there is only a slight chance of snow by late May, when moose give birth, and that concomitant increases in temperature typically would help initiate green-up of vegetation at that time (Fig. 6). Temperatures $>5^{\circ}\text{C}$ provide an index to plant growth in the Arctic (Chapin, 1983). Over the long term, such growth would be initiated by mid-May (Fig. 6), thereby providing high-quality forage by late May to support the nutritional demands of lactation.

In arctic and subarctic environments, the onset of winter may limit the time to provision young successfully, and in consequence, how early in spring young must be born to accrue sufficient body size and reserves to survive harsh conditions in winter (Bunnell, 1980; Rachlow and Bowyer, 1991). If moose timed births in response to long-term patterns of climate so that parturition was as early as possible, they could take advantage of the short growing season in the subarctic (Rachlow and Bowyer, 1994); this climatic constraint would help explain the high degree of synchrony in births, especially where animals are not gre-

garious around the time of parturition. Our data are consistent with this hypothesis, but we recognize we have not conducted a critical test of this idea.

Moose in North America, however, exhibit little variation in timing of parturition over ca. 15° of latitude (Schwartz, 1998). Conversely, moose in Fenoscandia show a delay in timing of births with increasing north latitude (Saether et al., 1996), a pattern noted for other cervids (Robinette et al., 1977). Indeed, a delay in phenology of plants with increasing north latitude is typical of some areas in both North America and Fenoscandia (Boer et al., 1990; Jaerinen, 1987; Robinette et al., 1977). Differences in timing of births for moose in these two regions likely are associated with the nature of the boreal forest in North America. Green-up throughout the boreal forest in Alaska occurs at a similar time (Markon et al., 1995). Structure and composition of plants in this community likely have moderating effects on snow melt (Larsen, 1980) and, hence, forage quality across North America. Moose throughout much of Fenoscandia occur in open coniferous forests (Saether et al., 1996), and warm ocean currents along the coast of Norway also may affect climate along a latitudinal gradient.

The difference in timing of births between North America and Fenoscandia cannot be attributed to fewer predators in Fenoscandia. Both wolves and grizzly bears have been extirpated from much of their original distribution in North America (Craighead and Mitchell, 1982; Mech, 1970), producing a patchy distribution in the primary predators of moose across that continent. Thus, we hypothesize that moose are tracking long-term patterns of climate to time reproduction throughout broad areas of the boreal forest in North America.

The moose is a keystone species that affects rates of nutrient cycling and plant succession in the boreal forest (Bowyer et al., 1997; Molvar et al., 1993; Pastor et al., 1988). Alterations in abundance of this

large herbivore hold the potential to cause perturbations in landscapes that they inhabit, including demographic changes in plants and other animals, and stability of predator-prey dynamics (Bowyer et al., 1997; Dale et al., 1994; Gasaway et al., 1992). Clearly, more research on the potential role of climatic change on the life-history patterns and population dynamics of large mammals is warranted if changes in fauna and plant-animal interactions are to be understood. Climatic change is predicted to be more extreme at high than moderate or low latitudes (Lashof and Ahuja, 1990). Potential effects of climatic change on biogeochemical cycling and on flora and communities of plants have been the focus of numerous studies (Chapin et al., 1995; McGuire et al., 1992, 1995). With the exception of Eastland and White (1991) and Post et al. (1997), however, little attention has been given to the responses of large, mammalian herbivores. We hypothesize that moose follow a strategy of timing births to track long-term patterns of climate, and subsequent forage availability and quality. We further hypothesize that moose would be affected by climatic change long before extensive alteration in vegetative communities occurred.

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