

EFFECTS OF MATERNAL CHARACTERISTICS AND CLIMATIC VARIATION ON BIRTH MASSES OF ALASKAN CARIBOU

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Understanding factors that influence birth mass of mammals provides insights to nutritional trade-offs made by females to optimize their reproduction, growth, and survival. I evaluated variation in birth mass of caribou (*Rangifer tarandus*) in central Alaska relative to maternal characteristics (age, body mass, cohort, and nutritional condition as influenced by winter severity) during 11 years with substantial variation in winter snowfall. Snowfall during gestation was the predominant factor explaining variation in birth masses, influencing birth mass inversely and through interactions with maternal age and lactation status. Maternal age effects were noted for females ≤ 5 years old, declining in magnitude with each successive age class. Birth mass as a proportion of autumn maternal mass was inversely related to winter snowfall, even though there was no decrease in masses of adult females in late winter associated with severe winters. I found no evidence of a hypothesized intergenerational effect of lower birth masses for offspring of females born after severe winters. Caribou produce relatively small offspring but provide exceptional lactation support for those that survive. Conservative maternal investment before parturition may represent an optimal reproductive strategy given that caribou experience stochastic variation in winter severity during gestation, uncertainty of environmental conditions surrounding the birth season, and intense predation on neonates.

Key words: birth mass, caribou, intergenerational effects, lactation, life-history strategy, maternal nutrition, *Rangifer tarandus*, reproductive investment, weather

The mass of a newborn is the expression of a female's adaptations to optimize the allocation of nutritional resources between survival of her offspring and her own future in a variable, and often hostile, environment (Robbins and Robbins 1979). For ungulates in northern latitudes, this becomes a nutritional paradox because most fetal growth occurs during the final months of winter when endogenous reserves are generally lowest (Chan-McLeod et al. 1999; Gerhart et al. 1996), and forage is poor in quality (Boertje 1990; Mautz 1978) and may be reduced in availability or acquired at a higher energetic cost because of persistent snow cover (Fancy and White 1985; Parker et al. 1984; Thing 1977). In addition, ungulate females must invest adequately in their offspring to meet the selective pressures of intense predation during the 1st few weeks of life (Adams et al. 1995a, 1995b; Ballard et al. 1981; Keech et al. 2000; Kunkel and Mech 1994; Singer et al. 1997).

The consequences of low birth mass and poor perinatal nutrition on growth, reproductive success, and survival have been documented across mammalian taxa (see Lindström 1999; Lummaa and Clutton-Brock 2002). For ungulates, investigators have shown that birth mass can be indicative of body size at later stages of life (Clutton-Brock et al. 1988; Keech et al. 1999; Kojola 1997; Schultz and Johnson 1995), is inversely correlated with the timing of sexual maturity (Forchhammer et al. 2001), and influences survival, particularly during the summer after birth (Clutton-Brock et al. 1982; Eloranta and Nieminen 1986; Gustafson et al. 1998; Thorne et al. 1976). Further, nutritional restriction during late pregnancy or after birth can result in effects that carry over to subsequent generations in that low-birth-mass females may produce lighter offspring themselves (Albon et al. 1987).

Birth mass of ungulates can be influenced by maternal characteristics including age, body size, and nutritional status during gestation. Young females tend to produce smaller offspring (Eloranta and Nieminen 1986; Ericsson et al. 2001; San José et al. 1999), whereas older, senescent females may (Clutton-Brock et al. 1982; Guinness et al. 1978) or may not (Ericsson et al. 2001). Birth mass has been correlated with maternal body size (Eloranta and Nieminen 1986; Kojola 1993;

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TABLE 1.—Summary of birth masses (kg) of caribou during 1987–1997 from the Denali caribou herd, Alaska.

Year	Winter snowfall ^a (cm)	Males				Females			
		\bar{X}	SE	Range	n	\bar{X}	SE	Range	n
1987	128	9.29	0.22	8.0–10.4	11	8.18	0.18	7.2–9.2	10
1988	121	8.93	0.25	6.4–10.4	21	8.03	0.28	5.9–9.9	13
1989	246	7.80	0.22	5.9–9.5	20	7.52	0.23	5.8–9.2	20
1990	226	7.84	0.22	6.4–9.2	17	6.80	0.24	4.7–8.3	16
1991	394	6.71	0.25	4.7–7.9	15	6.52	0.18	4.4–8.1	21
1992	323	7.85	0.17	6.0–9.7	27	7.25	0.26	3.9–8.9	23
1993	394	7.75	0.20	6.4–9.7	17	6.96	0.24	4.4–8.6	20
1994	280	8.10	0.15	6.0–9.2	33	7.34	0.16	5.4–9.2	31
1995	177	7.75	0.20	5.4–9.4	28	7.50	0.18	5.4–9.9	39
1996	166	8.16	0.22	5.9–10.7	29	7.97	0.13	6.2–10.0	39
1997	174	8.39	0.18	5.9–10.2	26	8.14	0.13	6.7–10.4	35
\bar{X}		8.04	0.07	4.7–10.7	244	7.50	0.07	3.9–10.4	267

^a Snowfall during September–May in winter before birth.

Rognmo et al 1983). Effects of nutrition on birth mass in ungulates have been demonstrated in captive experiments (Peart 1967; Rognmo et al. 1983; Thorne et al. 1976; Verme 1963) and by evaluating relationships with environmental variation or changes in population density (Anderson and Linnell 1997; Clutton-Brock et al. 1982, 1992; Forchhammer et al. 2001; Guinness et al. 1978; Sarno and Franklin 1999). In addition, females lactating during gestation may produce smaller offspring (Clutton-Brock et al. 1989). Further, male offspring are commonly heavier at birth than females (Birgersson and Ekvall 1997; Clutton-Brock et al. 1982; Eloranta and Nieminen 1986; Kojola 1997; San José et al. 1999), although there are exceptions (Byers 1997; Fairbanks 1993; Sarno and Franklin 1999).

Most studies of birth mass variation in ungulates have been conducted on food-limited populations with few natural predators (e.g., Albon et al. 1983, 1987; Clutton-Brock et al. 1982, 1992; Ericsson et al. 2001) or captive populations (e.g., Birgersson and Ekvall 1997; Eloranta and Nieminen 1986; Kojola 1993, 1997; Pélabon 1997; Thorne et al. 1976;). During 1987–1997, I studied the production and survival of caribou (*Rangifer tarandus*) calves in Denali National Park, Alaska, where caribou occur at low densities (≤ 0.3 individuals/km²) and experience losses of $\leq 78\%$ of their young, primarily to predation, during the month after birth (Adams et al. 1995a, 1995b). Such high levels of neonatal predation may contribute to improved nutritional condition of reproductive-age females because most females do not bear the costs of lactation (Adams and Dale 1998a). Although these caribou are generally in superior nutritional condition (Adams et al. 1995b; Adams and Dale 1998a), my studies encompassed a period of wide variation in winter snowfall that affected their nutritional status as demonstrated by effects on productivity (Adams and Dale 1998a, 1998b), postnatal growth and development (Adams 2003), and survival of young (Adams et al. 1995a, 1995b). As a part of these studies, more than 500 newborn caribou were weighed and I observed substantial variation in the masses obtained. For this paper, I describe the variation in birth mass in the Denali caribou herd during 11 years and examine factors that may influence birth mass, including offspring sex, maternal attributes (age, cohort, body mass, and lactation status), and

variation in winter snowfall as it influenced maternal nutritional condition during gestation.

MATERIALS AND METHODS

During this study, the Denali caribou herd used about 10,000 km² in and adjacent to Denali National Park and was well below historic population levels of $>20,000$ caribou (Murie 1944). In autumn 1986, the herd was composed of about 2,500 caribou and was increasing at 8%/year during a period of below-average winter snowfalls (Adams et al. 1995a; Adams and Mech 1995). With heavier snowfalls beginning in winter 1988–1989, growth of the herd stopped, peaking at 3,200 caribou in autumn 1989. The 4 winters during 1990–1994 were particularly severe, with snowfalls in the upper quartile of winters since 1924–1925 and including 2 of the 4 greatest snowfalls on record. By autumn 1994, the Denali herd declined by 34% to about 2,100 caribou. After the 1993–1994 winter, snowfall patterns returned to near-average conditions for the remainder of this study and the decline in caribou numbers halted.

The range of the Denali caribou herd included much of Denali National Park (63°N, 150°W), ranging from alpine habitats (800–2,200 m elevation) to taiga, boreal forest, and tussock (*Eriophorum*) tundra habitats (<800 m elevation). Approximately 2,000 moose (*Alces alces*) and 1,700 Dall's sheep (*Ovis dalli*) also inhabited the caribou herd's range (United States National Park Service, in litt.). Caribou were preyed upon by gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*)—Adams et al. 1995a, 1995b; Murie 1944).

The region has a subarctic, montane climate with annual precipitation averaging 38 cm deposited primarily as snow during late September to mid-May. During this study, total winter snowfall, measured at Denali National Park headquarters on the eastern edge of my study area, varied from 121 to 394 cm (Table 1). Since 1924, winter snowfall has averaged 207 cm, ranging from 86 to 441 cm. During my study most of the snow fell early in the winter, with 50% of the total annual snowfall occurring by mid-December. Snow accumulation on the ground approached maximum depths by mid-January and remained relatively constant throughout the remainder of the winter until the onset of snow melt after 15 April.

My research employed aerial radiotelemetry to monitor radio-collared adult (≥ 2 -year-old) caribou females daily during the birth season (May–early June—Adams and Dale 1998b) until they gave birth. Their offspring were radiocollared shortly after birth (≤ 2 days) to

evaluate characteristics of calf mortality (Adams et al. 1995a, 1995b). Captures and handling reported here comply with current guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

During 1986–1997, I captured 120 10-month-old females from the 1986–1995 cohorts and 57 older females via helicopter darting (Adams and Dale 1998a) during autumn (22 September–20 November) and late winter (8–25 March), fitted them with radiocollars, and weighed them to the nearest 0.5 kg. Instrumented females were recaptured every 3–4 years to replace radiocollars before battery exhaustion and were reweighed. Ages of females were either known (original capture at 10 months of age) or estimated from cementum annuli of a canine tooth extracted at capture or recovered at death (Miller 1974; Reimers and Nordby 1968). For the 1986–1995 cohorts that reached adulthood during this study, I radiocollared an average of 12 individuals (range 4–16) per cohort at 10 months of age. Ages of adult females herein refer to ages at the time of parturition, unless otherwise noted.

During each birth season, I monitored the reproductive status of 30–83 radiocollared adult females ($\bar{X} = 64$) with the goal of capturing all the neonates born to this sample. When a neonate was 1st observed with a radiocollared female, a person was dropped off via helicopter within a few meters of the caribou and captured the calf by hand. If the helicopter could not land in the immediate vicinity of the target caribou because of steep terrain or tree cover, 1 or 2 people were dropped off within 400 m and the helicopter slowly herded the mother and offspring toward the hidden capture crew or directed the capture crew to the calf via handheld radio. If a neonate appeared to be recently born (e.g., wet coat and unable or barely able to stand), I waited several hours to conduct the capture to allow sufficient time for the bond to develop between the offspring and its dam. Neonates were radiocollared and then weighed to the nearest 0.25 kg with a handheld spring scale and a cloth strap positioned around the animal's chest. Each person handling calves wore clean latex gloves and used a clean cloth weighing strap for each capture to minimize scent transfer among individuals. The sex of each neonate was determined and its age was estimated based on previous observations of its radiocollared mother, its posture and coordination, and characteristics of its umbilicus and hooves (Adams et al. 1995a). Most of the neonates that were weighed were <1 day old at capture ($n = 322$), whereas the remainder were estimated to be 1 or 2 days old ($n = 163$ and 26, respectively). The entire capture and handling procedure took less than 2 min and study-induced abandonment was rare ($n = 2$ of 511 captures).

To estimate birth masses of offspring captured after the day of birth, investigators commonly assume a daily rate of gain and subtract the increment for each day of estimated age (Adams et al. 1995a; Clutton-Brock et al. 1982, 1992; Fairbanks 1993; Keech et al. 1999). However, it is unlikely that the rate of growth is the same for all offspring given the 3- to 4-fold variation in birth mass common in these studies. Therefore, I assumed a proportional daily growth increment based on linear regression of capture mass on estimated age at capture (birth mass [kg] = $7.77 + 0.51 \times \text{age at capture [days]}$; $r^2 = 0.066$, $F = 35.88$, $d.f. = 2, 509$, $P < 0.001$). To estimate birth mass of caribou calves that were 1 or 2 days old at capture, I reduced capture mass by 6.2% and 11.6%, respectively. The coefficient of variation for mass at capture (14.77%) declined little with this age correction (14.34%), indicating that variability associated with age at capture was relatively inconsequential compared to the overall variability in birth mass.

I evaluated the sex composition of my sample of calves via chi-square analyses, employed *t*-tests and analysis of variance procedures to compare means among 2 or more categories, respectively, and used simple linear regression to evaluate trends in birth masses relative to

continuous variables. For these statistical tests, I considered $P \leq 0.05$ indicative of a significant result.

I applied multiple linear regression to simultaneously evaluate calf sex, maternal age, and winter snowfall before birth as factors influencing birth mass. Offspring sex and maternal age were represented by indicator variables, whereas winter snowfall was treated as a continuous variable. I limited maternal age classes to 2, 3, 4, 5, and ≥ 6 years old based on patterns of female growth (see below; Dauphiné 1976) and relationships with birth masses and maternal age reported below. All 2-factor interactions were included. I selected the most parsimonious regression model for which Mallows' C_p was less than or equal to the number of parameters (Weisberg 1985) and coefficients differed from 0 ($P \leq 0.100$).

For analyses of lactation status and intergenerational effects, I started with the parameters selected in the multiple regression analysis of offspring sex, maternal age, and winter snowfall and evaluated whether additional variables significantly improved the regression model by meeting the specified C_p and P -value criteria. To evaluate lactation status, I used only those neonates born to mothers that I knew were sexually mature (had previously produced an offspring) and I knew whether or not they had an offspring at heel the previous September. I tested an indicator variable for lactation status and an interaction term for lactation status and winter snowfall. To evaluate intergenerational effects, I hypothesized that winter snowfall before the birth of maternal cohorts would have a significant inverse relationship with birth mass. Following Albon et al. (1987), I also compared mean birth masses of calves born to each maternal cohort, controlling for effects of calf sex (female), maternal age (≥ 6 years old), and winter snowfall (long-term average = 207 cm) identified in the multiple regression analyses, with the mean birth masses of females for each of the maternal cohorts born during my study (1987–1994).

RESULTS

I weighed 511 neonates during 1987–1997, averaging 46 neonates/year (Table 1). The sex ratio of the offspring (267 females to 244 males) did not differ from parity overall ($\chi^2 = 1.04$, $d.f. = 1$, $P = 0.309$) or vary among years ($\chi^2 = 7.17$, $d.f. = 10$, $P = 0.709$). Neonates that were weighed were born to 136 radiocollared females averaging 3.8 neonates/cow \pm 2.0 *SD* (range = 1–11 neonates).

Offspring sex, maternal age, and winter snowfall effects.—Overall, birth mass averaged 7.8 kg \pm 1.1 *SD*, but varied from 3.9 to 10.7 kg (Table 1). Males were 0.54 kg heavier at birth than females on average ($\bar{X} = 8.04$ kg versus 7.50 kg.; $t = 5.64$, $d.f. = 509$, $P < 0.001$). Birth masses varied significantly among years ($F = 12.91$, $d.f. = 10, 500$, $P < 0.001$), with annual means ranging from 6.6 kg in 1991 to 8.8 kg in 1987, and were inversely correlated with winter snowfall before birth ($r^2 = 0.135$, $F = 79.21$, $d.f. = 1, 509$, $P < 0.001$; Fig. 1).

Birth mass varied significantly with maternal age ($F = 5.42$, $d.f. = 14, 496$, $P < 0.001$; Fig. 2). For each age class ≤ 5 years old, offspring were significantly lighter than those born to all females older than that age class ($t \geq 2.40$, $P \leq 0.017$), whereas birth masses did not differ among age classes ≥ 6 years old ($F = 0.63$, $d.f. = 10, 279$, $P = 0.789$). Although females ≥ 14 years old exhibited reduced productivity (Adams and Dale 1998a), the average birth mass of their offspring ($n = 13$) was identical to that of females 6–13 years old (8.0 kg; $t = 0.00$, $d.f. = 288$, $P = 0.997$).

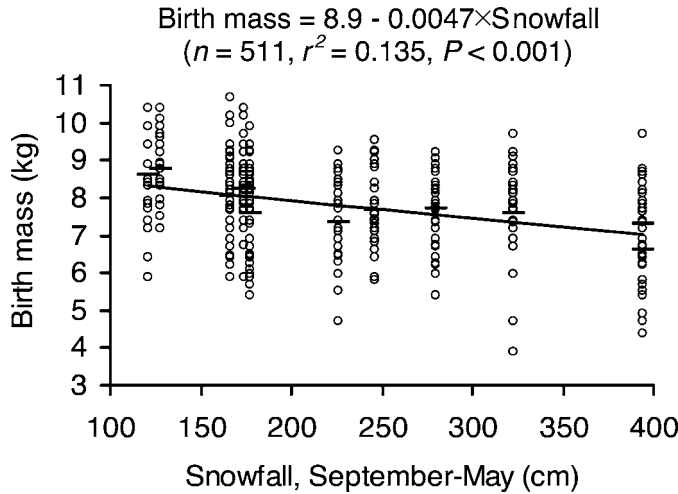


FIG. 1.—Birth masses of caribou calves relative to snowfall during the winter before their birth (horizontal bars indicate annual means) during 1987–1997, Denali National Park, Alaska.

In the multiple regression analyses of offspring sex, maternal age, and winter snowfall (Table 2), birth mass was significantly related to all 3 factors. As in the previous univariate analyses, male young were significantly heavier than females by 0.54 kg. Birth masses were inversely related to winter snowfall and predicted values declined by 15% over the range of winter snowfalls during the study. Offspring of 2- and 3-year-old females were significantly lighter than those born to older females. Further, no 2-year-olds produced young in 1991–1993 when winter snowfalls exceeded 300 cm ($n = 34$). For 4- and 5-year-olds, interaction terms with winter snowfall were included in the regression model, indicating that declines in birth masses of their offspring were exacerbated as winter snowfall increased (20% and 18% declines, respectively, over the

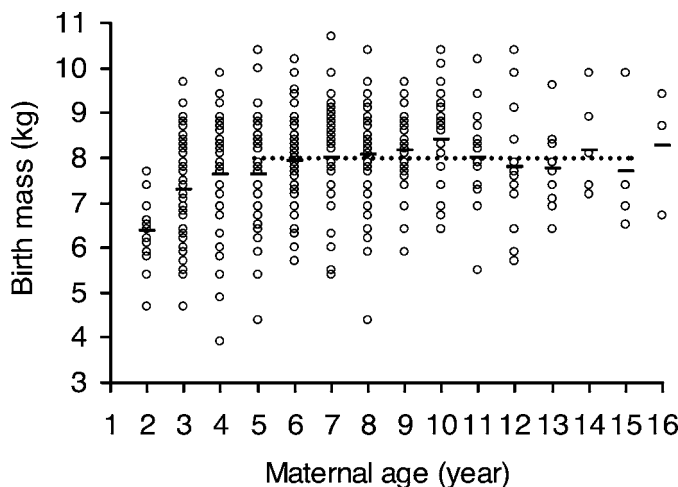


FIG. 2.—Relationship between birth masses of caribou calves ($n = 511$) and the ages of their dams at parturition during 1987–1997, Denali National Park, Alaska. Horizontal bars indicate mean birth masses for each maternal age class. Birth masses did not differ among females ≥ 6 years of age ($F = 0.63$, $d.f. = 10, 279$, $P = 0.789$); dotted line is the grand mean for these age classes (8.0 kg).

TABLE 2.—Regression results for relationships of birth mass of caribou with offspring sex (0 = female, 1 = male); winter snowfall before birth (September–May snowfall in cm); and indicator variables of maternal age for females 2, 3, 4, and 5 years of age at the time of parturition, Denali National Park, Alaska, 1987–1997.

Variable	β_x	t	P
Selected model ($n = 511$, Adjusted $R^2 = 0.308$)			
Constant	8.78	68.28	<0.001
Sex	0.54	6.58	<0.001
Snow	-0.0045	8.68	<0.001
Maternal age = 2	-1.82	8.51	<0.001
Maternal age = 3	-0.61	4.89	<0.001
Snow \times maternal age = 4	-0.0014	2.83	0.005
Snow \times maternal age = 5	-0.00075	1.65	0.099
Variables not selected			
Maternal age = 4	0.34	0.737	
Maternal age = 5	0.08	0.934	
Snow \times maternal age = 2	0.71	0.477	
Snow \times maternal age = 3	0.48	0.633	
Sex \times maternal age = 2	0.91	0.364	
Sex \times maternal age = 3	0.64	0.521	
Sex \times maternal age = 4	0.55	0.581	
Sex \times maternal age = 5	0.51	0.613	
Sex \times snow	0.49	0.624	

observed range of winter snowfall). Although birth masses were influenced by offspring sex, winter snowfall before birth, and maternal age, these variables and their interactions accounted for less than one-third of the observed variation (Table 2), with winter snowfall (adjusted $r^2 = 0.133$) alone contributing nearly one-half of the explanatory resolution.

Effects of lactation.—Of the 511 neonates weighed, 393 were born to females known to be sexually mature (i.e., previously produced an offspring) and for which presence or absence of an offspring at heel the previous September also was known. For these young, the interaction between lactation status and winter snowfall was a significant improvement ($\beta_x = -0.0018$, $t = 3.30$, $d.f. = 1$, $P = 0.001$) to the previous multiple regression model (the indicator variable for 2-year-olds was dropped because none were sexually mature), whereas lactation status alone was not ($t = 0.33$, $d.f. = 1$, $P = 0.744$). To illustrate this interaction, after the winter with the least snow (1988), birth masses were identical for sexually mature females that were lactating the previous autumn and those that were not (8.8 kg; $t = 0.01$, $d.f. = 24$, $P = 0.505$), whereas they differed by 0.9 kg (6.2 kg and 7.1 kg, respectively; $t = 1.78$, $d.f. = 63$, $P = 0.040$) after the winters with the most snow (1991 and 1993).

Birth mass versus maternal body mass.—I obtained 138 body masses of females ≥ 3 years old at date of capture ($n = 101$ females; 35 females were weighed 2 times and 1 female was weighed 3 times, ≥ 3 years apart), including 75 from autumn and 63 from late winter. Three-year-old females were significantly lighter than older females in both seasons (Table 3), whereas body masses did not differ among females ≥ 4 years old (females ≥ 10 years old pooled; autumn, $F = 0.49$, $d.f. = 6, 38$, $P = 0.813$; late winter, $F = 0.80$, $d.f. = 6, 43$, $P = 0.572$). Body masses in autumn did not differ among years for 3-year-olds ($F = 1.26$, $d.f. = 4, 25$, $P = 0.314$) or older females

TABLE 3.—Body masses (kg) of female caribou ≥ 3 years old at time of capture relative to age, winter snowfall (September–May snowfall), and season during 1986–1997, Denali National Park, Alaska.

	\bar{X}	SE	n	t	P
Age (3 years old versus ≥ 4 years old)					
Autumn					
3 years old	112.6	1.51	30		
≥ 4 years old	121.8	1.50	45	4.12	<0.001
Late winter					
3 years old	104.4	2.20	13		
≥ 4 years old	115.8	1.20	50	4.36	<0.001
Snowfall (winter snowfall ≤ 300 cm versus >300 cm)					
3 years old; late winter					
≤ 300 cm snow	109.1	1.96	8		
>300 cm snow	96.8	1.91	5	4.23	0.001
≥ 4 years old; late winter					
≤ 300 cm snow	115.5	1.11	41		
>300 cm snow	116.9	4.61	9	0.43	0.671
Season (autumn versus late winter [by snowfall class for 3-year-olds])					
3 years old					
Autumn	112.6	1.51	30		
Late winter; ≤ 300 cm snow	109.1	1.96	8	1.13	0.267
Late winter; >300 cm snow	96.8	1.91	5	4.15	<0.001
≥ 4 years old					
Autumn	121.8	1.50	45		
Late winter	115.8	1.20	50	3.13	0.002

($F = 1.43$, d.f. = 5, 39, $P = 0.235$). In late winter, 3-year-olds were lighter during severe winters, whereas masses of older females did not differ with winter severity (Table 3).

Birth masses of offspring were positively correlated with masses of their mothers in autumn, near the time of conception ($r^2 = 0.221$, $F = 12.50$, d.f. = 1, 44, $P = 0.001$), averaging $6.5 \pm 1.5\%$ SD of autumn maternal mass. Birth mass as a proportion of maternal mass did not differ significantly between females weighed when 3 years old (4 years old at parturition) and older females (6.3% versus 6.7%, respectively; $t = 1.34$, d.f. = 44, $P = 0.187$), but declined significantly with increasing winter snowfall ($r^2 = 0.332$, $F = 21.89$, d.f. = 1, 44, $P < 0.001$), ranging from a predicted value of 7.7% after the winter with lowest snowfall to 5.6% after the most severe winters.

Birth masses of young were only weakly correlated with the masses of their mothers in late winter, approximately 2 months before birth ($r^2 = 0.081$, $F = 4.04$, d.f. = 1, 46, $P = 0.050$) and averaged $6.7\% \pm 0.9\%$ SD of their mother's late-winter mass. Birth mass as a proportion of maternal mass did not differ significantly between females weighed when 3 years old (4 years old at parturition) and older females (7.0% versus 6.7% respectively; $t = 0.90$, d.f. = 46, $P = 0.375$), among years ($F = 0.36$, d.f. = 6, 41, $P = 0.899$), or with winter snowfall ($r^2 = 0.000$, $F = 0.01$, d.f. = 1, 46, $P = 0.926$). However, unlike the entire sample of calves I weighed, this small group of calves exhibited no significant decline in birth mass with increasing winter snowfall ($r^2 = 0.003$, $F = 0.15$, d.f. = 1, 46, $P = 0.701$).

Intergenerational effects.—The neonates I weighed were born to females from 20 cohorts (1974, 1976–1994). Winter

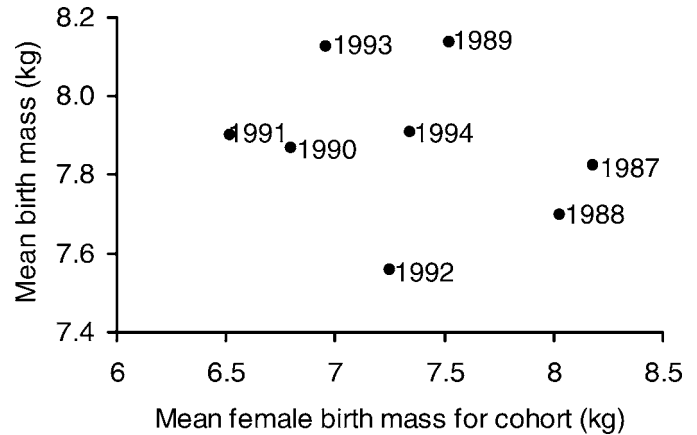


FIG. 3.—Mean birth masses of offspring born to the 1987–1994 maternal cohorts (controlling for effects of offspring sex, maternal age, and winter snowfall) versus mean birth mass of females in their mothers' cohort, Denali caribou herd, Alaska.

snowfall before birth of maternal cohorts met criteria to be added to the regression model ($t = 1.87$, d.f. = 1, $P = 0.062$). However, the regression coefficient was positive ($\beta_x = 0.00084$) and therefore counter to the hypothesized decline in birth mass of young produced by mothers born after increasingly severe winters. In analyses comparable to Albon et al. (1987), I detected no relationship between the mean birth masses of calves born to each cohort and the mean birth mass of the maternal cohorts themselves ($r^2 = 0.066$, $F = 0.42$, d.f. = 1, 6, $P = 0.539$; Fig. 3).

DISCUSSION

Birth masses of Denali caribou varied widely in association with variation in winter snowfall experienced during this study. Winter snowfall was the predominant explanatory variable, with an inverse association with birth mass overall, as well as interactions with maternal age and lactation status. Other authors have reported effects of climatic variation on birth mass for free-ranging ungulates (Albon et al. 1983, 1987; Anderson and Linnell 1997; Bergerud 1975; Forchhammer et al. 2001). Although winter severity influenced female nutritional status during gestation to bring about variation in birth mass, effects of winters with abundant snowfall were exacerbated for females ≤ 5 years old and those that were lactating.

Even though the Denali caribou herd occurred at low density (0.2–0.3 individuals/km²), adult females were large bodied compared to other Alaskan caribou, and productivity was generally high (Adams and Dale 1998a), climatic variation exhibited pervasive effects on calf production and survival. Components of my research have shown that increased winter severity before conception, combined with the shorter growing seasons after severe winters (Adams and Dale 1998b), reduced reproductive performance (Adams and Dale 1998a) and delayed timing of parturition (Adams and Dale 1998b), whereas severe winter conditions during gestation decreased birth mass (this study), postnatal growth and development

(Adams 2003), and calf survival from birth to autumn (Adams et al. 1995a, 1995b).

Effects of maternal age on birth mass were noted only for females ≤ 5 years old. Young females face the competing nutritional demands of their own growth while attempting to reproduce (Charnov 1991). With each successive age class, the nutritional priorities for growth are lessened and more resources can be directed to reproduction, as evidenced by decreasing influences of maternal age on productivity and birth mass. In this population some 2-year-olds produced young, but productivity of the age class was low (27%—Adams and Dale 1998a) and offspring were 22% smaller than those of fully mature females (≥ 6 years old). Further, 2-year-olds tended to produce offspring late in the calving season (Adams and Dale 1998b) and did not reproduce as winter severity increased (Adams and Dale 1998a). Three-year-olds produced young more consistently (Adams and Dale 1998a) and their offspring were markedly larger than those of 2-year-olds, averaging only about 8% smaller than calves of mature females. Four- and 5-year-olds closely approached or attained their maximum body sizes, and their ability to produce young of comparable mass to older females depended on winter severity during gestation.

I detected no decline in birth mass of young born to females ≥ 14 years old, even though their productivity was reduced (Adams and Dale 1998a). Similarly, Ericsson et al. (2001) reported reproductive senescence with no decline in birth mass for a moose population that was intensively harvested in Sweden. However, in food-limited populations, old females produce lighter offspring (Clutton-Brock et al. 1982, 1992). Where forage resources are limited and competition is keen, females generally exist at a lower plane of nutrition, but old females may be at a disadvantage with prime-age competitors, further degrading their nutritional status. With reduced competition for forage, old females may be less affected by competition and are therefore more likely to acquire the necessary nutritional currency to invest in offspring of comparable size to other females.

Birth mass was more strongly correlated with maternal mass in autumn than in late winter. Further, birth mass expressed as a proportion of autumn maternal mass declined with increasing winter severity, indicating that females invested less of their autumn nutritional reserves in offspring during severe winters. Surprisingly, the body masses of females ≥ 4 years old in late winter did not decline in severe winters. This indicates that females, at least in these age classes, may have been “selfish” (Festa-Bianchet and Jorgenson 1998) and reduced their reproductive investment in winters with limited access to forage, in favor of maintaining their own body condition through to the end of winter. Alternatively, females may have maintained body mass to mid-March regardless of winter severity and the nutritional restriction in severe winters took its toll on their body reserves in the final 2 months of winter. This seems unlikely because winter severity was usually well established by mid-January and it would require that, during severe winters, females lost a sizable proportion of their mid-March masses in the 2 months leading to parturition.

Although I detected an intergenerational effect on birth mass relative to winter snowfall before birth of maternal cohorts, the

results were the opposite of what I expected. Females born after severe winters exhibited a tendency to produce slightly larger calves (<0.4 kg increase over the range of winter snowfall), rather than the smaller offspring hypothesized. Further, for red deer (*Cervus elaphus*) on the Isle of Rum, Albon et al. (1987) showed a striking correlation between the mean birth mass of each maternal cohort and the birth masses of offspring born to that cohort, whereas I found no such relationship here in similar analyses. The red deer population studied by Albon et al. (1987) occurred at densities nearly 2 orders of magnitude greater (Clutton-Brock et al. 1982) than the Denali caribou herd, and by the later stages of gestation in early spring, all hinds were in relatively poor condition (Clutton-Brock et al. 1987). Intergenerational effects noted for red deer likely resulted because “intense competition for resources maintains or exaggerates initial differences in growth and resource access” (Albon et al. 1987:80). Conversely, caribou in Denali National Park did not experience chronic competition for forage, and nutritional restriction even during the most severe winters was short-lived, lasting only a few months. Although these caribou experience sufficient nutritional deficits to decrease birth masses after winters with abundant snow, the negative effects did not carry over to the next generation. Surviving individuals had ample opportunity to compensate for their own low birth mass, although there may be hidden costs of such compensation (Metcalf and Monaghan 2001). Alternatively, the nutritional effects that calves experienced in utero were not sufficient to invoke intergenerational effects of prenatal undernutrition (Lummaa and Clutton-Brock 2002).

Compared to other ungulates of small to moderate size (adult females < 200 kg), caribou produce offspring that are rather small relative to maternal body mass (Oftedal 1985; Robbins and Robbins 1979). Keeping reproductive investment low before parturition may be an optimal life-history strategy given that caribou inhabit stochastic environments that affect juvenile survival substantially more than adult survival (Hirshfield and Tinkle 1975; Lindström 1999). In addition to the substantial variation in winter severity at the northern latitudes where they occur, caribou face uncertainty in the timing of snow ablation and the onset of plant growth during each calving season (Adams and Dale 1998b) that can influence their nutritional status at a critical time of the year. Further, many populations experience intense neonatal losses to predation that vary widely with winter severity (Adams et al. 1995a, 1995b). However, offspring that survive the gauntlet of nutritional uncertainty and intense predation receive maternal investment via lactation that exceeds that of other ungulates of similar size (Robbins and Robbins 1979). By generally producing small offspring, and further restraining their late gestation investment in severe winters, caribou females conserve nutritional resources that may enhance their own survival or that can be invested in offspring should they survive beyond a couple of weeks. Given that an individual female will experience a variety of winter conditions in her lifetime, such phenotypic plasticity would be selected for by increasing maternal investment in offspring that are most likely to survive to reproduce (Festa-Bianchet and Jorgenson 1998).

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