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Annual variation in maternal age and calving date generate cohort effects in moose (*Alces alces*) body mass

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Abstract A general feature of the demography of large ungulates is that many demographic traits are dependent on female body mass at early ages. Thus, identifying the factors affecting body mass variation can give important mechanistic understanding of demographic processes. Here we relate individual variation in autumn and winter body mass of moose calves living at low density on an island in northern Norway to characteristics of their mother, and examine how these relationships are affected by annual variation in population density and climate. Body mass increased with increasing age of their mother, was lower for calves born late in the spring, decreased with litter size and was larger for males than for female calves. No residual effects of variation in density and climate were present after controlling for annual variation in mother age and calving date. The annual variation in adult female age structure and calving date explained a large part (71–75%) of the temporal variation in calf body mass. These results support the hypotheses that (a) body mass of moose calves are affected by qualities associated with mother age (e.g. body condition, calving date); and (b) populations living at low densities are partly buffered against temporal fluctuations in the environment.

Keywords Calf sex · Density · Climate · Maternal effects · Mixed effect models · Cohort effects

Introduction

Body mass can explain a large part of the variation in individual fitness in mammals (Bérubé et al. 1999; Gaillard et al. 2000a) and hence may influence their population dynamics (e.g. Gaillard et al. 2000b; Hewison and Gaillard 2001). Among ungulates, body mass affects social status (e.g. Veiberg et al. 2004) and are found to be positively related with fighting and mating success among males (e.g. Clutton-Brock et al. 1988; McElligott et al. 2001). Large body mass is also associated with high fecundity (Gaillard et al. 1992; Sæther and Haagenrud 1985; Sand 1996; but see Gaillard et al. 2000b) and larger individuals tend to mature earlier than smaller individuals (e.g. Sæther and Heim 1993; Garel et al. 2005). Variation in adult size is in turn influenced by body growth and size in early life (Albon et al. 1987; Festa-Bianchet et al. 2000; Beckerman et al. 2002), indicating that strong compensatory growth from juvenile to adulthood is rare in ungulates (Gaillard et al. 2003; but see Toïgo et al. 1999). Identifying factors affecting the variation in juvenile body mass therefore is important for understanding evolutionary and demographic processes in ungulate populations (e.g. Kruuk et al. 1999; Réale and Boussès 1999; Coulson et al. 2003).

Variation in juvenile body mass is usually explained by spatio-temporal variation in the environment (Sæther 1997) and/or by parental characteristics (Skogland 1984; Coté and

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Festa-Bianchet 2001; Don Bowen et al. 2001). In temperate ungulates, the feeding conditions during summer are important for early growth (Sæther 1997). Thus, it is of vital importance for body growth whether a young is raised in a good or a poor habitat (Pettorelli et al. 2001; Sæther and Heim 1993). Similarly, temporal variation in density and climate may affect the food quality and per-capita quantity of food (Sæther 1997). Such year-effects can have a strong impact on the variation in body mass in ungulates (e.g. Post et al. 1997; Coltman et al. 1999; Pettorelli et al. 2002), and have the potential to generate cohort effects that may have long-lasting fitness consequences (Albon et al. 1987; Rose et al. 1998; Gaillard et al. 2003; Solberg et al. 2004).

There is also some evidence that cohort effects in fitness-related traits is the result of annual variation in phenotypic characteristics of their parents (Clutton-Brock and Albon 1989; Beckerman et al. 2002). Such parental effects include maternal effects, which are defined as the influence of the mother's phenotype or her home range on the phenotype of her offspring (Kirkpatrick and Lande 1989; Mousseau and Fox 1998). Maternal effects transmit individual life-history responses between generations and may have strong effects on the distribution of phenotypes in a population (Wolf et al. 1998; Beckerman et al. 2002). As a consequence, variation in age, body condition and social status of mothers may affect the size and quality of their offspring (Skogland 1984; Coté and Festa-Bianchet 2001; Landete-Castillejos et al. 2005), and in turn their fitness (e.g. Beckerman et al. 2002).

In this study, we examined the influence of maternal characteristics, such as mother age and calving date, on the variation in body mass of moose *Alces alces* L. calves on the island of Vega in northern Norway (Sæther et al. 2003, 2004) while simultaneously controlling for variation in litter size and calf sex. Maternal body condition is often found to be positively related to age in ungulates (e.g. roe deer: Hewison and Gaillard 2001; for moose: Sæther et al. 2001; Solberg et al. 2004), and, accordingly, older mothers are assumed to have more body reserves available for calf production than younger mothers. Similarly, maternal qualities may have an effect on calf body mass indirectly by influencing on their date of birth (Clutton-Brock et al. 1982). Both mothers and offspring are dependent on high-quality food for optimal growth, and since the quality of plants deteriorate during the growing season (Robbins 1983; White 1983), it may be beneficial for the offspring to be born at some optimal date with respect to the quality and quantity of food plants (Klomp 1970; Bunnell 1982; Oftedal 1985; Rutberg 1987; Albon and Langvatn 1992; Coté and Festa-Bianchet 2001).

Based on the large variation in female age and calving date in our study population, we predicted large variation in calf body mass within years. Moreover, because the age structure may vary extensively between years in harvested populations (Solberg et al. 1999; see Sæther et al. 2003 for our population), we also examined the extent of annual differences in calf body mass that were related to temporal variation in maternal phenotypic characters compared to population density and climate.

Materials and methods

Study area

Vega (65°40′N, 11°55′E) is an island with an area of 119 km^2 located off the coast of Helgeland in northern Norway (Fig. 1). The landscape is dominated by a mixture of agricultural areas, marsh, and moor land dominated by heather (*Calluna vulgaris*), interspersed with small areas of deciduous forest and short-grown pine (*Pinus sylvestris*) forests. There is a steep mountainous region in the south-western part of the island, not utilised by, and assumed to be uninhabitable for moose, leaving 80 km^2 of the island as moose habitat.

The moose population

The first moose arrived at Vega in 1985 when two yearling females and one yearling male swam across from the mainland and established themselves on the island (Sæther et al. 2003). The population multiplied in the following years and by the time the study started in 1992, the population numbered 24 animals. During the winter of 1992, we immobilised and radio marked 18 moose on the island by the use of a helicopter. Another two were immobilised from the ground and radio marked the following spring and summer, whereas the last four adult moose, as well as all new calves, were radio marked using a helicopter during the winter of 1993. Each of the following winters, except 2003, we continued radio marking calves and immigrants, and changed radio collars on animals with malfunctioning transmitters. With this procedure a high proportion of moose (>90%) on the island have been radiocollared during the entire study period.

Hunting started in 1989, and until 1993 a small number of animals were shot each autumn (Sæther et al. 2001). Since 1994, the population has been kept within an estimated winter size of 29–43 moose by harvesting (Sæther et al. 2003). Mortality outside the hunting season is low (~5%), and smaller than recorded in other moose populations in northern Norway (Stubsjøen et al. 2000).

The study at Vega was initiated mainly to examine the effects of skewed adult sex ratios on fecundity and calving dates in a moose population (Sæther et al. 2001). To

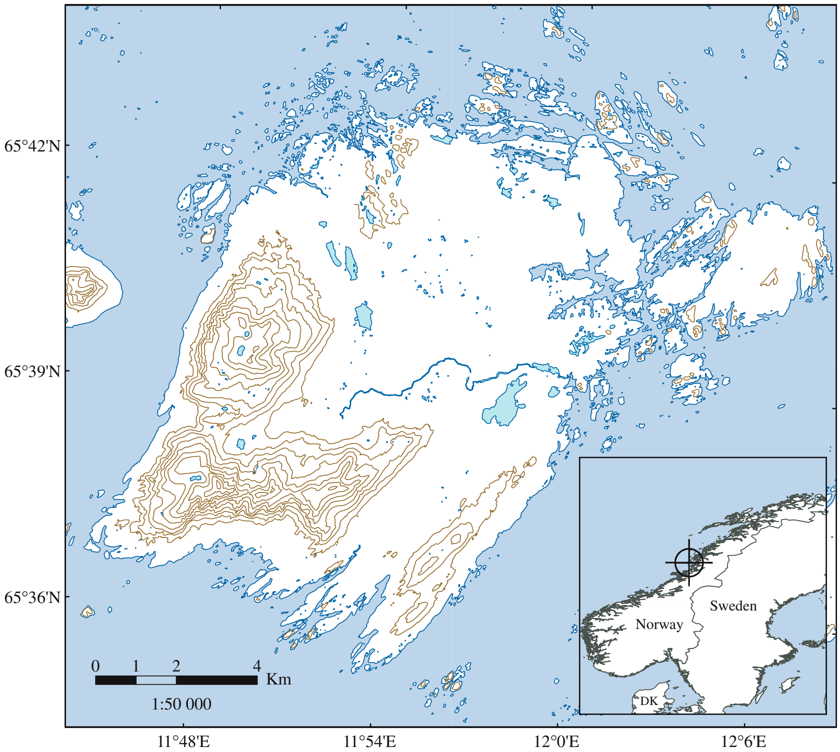

Fig. 1 The location of the study area, the island of Vega (65°40′N–11°55′E)

achieve this, the sex and age structure of the population was manipulated by selective harvesting during the period 1994–1999 (Sæther et al. 2003). The adult females on the island responded to this manipulation by delaying their calving date by as much as 9 days on average, which was interpreted to be caused by delayed conception during the previous rutting season due to the low proportion of appropriate males (Sæther et al. 2003), and led to relatively large variation in calving date. Similarly, the manipulation probably distorted the age structure of both males and females beyond what would normally have been observed. The population manipulation may therefore have increased the chance to find the expected effects because of the larger variance, but we have no reasons to believe that it otherwise has influenced on the results.

Data collection

When first captured (in January–March), all calves were radio-collared, ear-tagged and weighed to the nearest kilogram (±2 kg) with a digital scale installed in the helicopter or by a manual scale hanging from the helicopter. The two scales were compared and calibrated. In addition, carcass mass was measured on all calves harvested during the autumn hunting season. Carcass mass is equal to body mass minus the head, skin, metapodials, bleedable blood, and viscera, and constitutes ~56% of total body mass at Vega (E. J. Solberg, unpubl. data, Fig. 2a, b).

Age and reproduction data were available from 32 adult (≥2.5 years old) radio-collared females, from which body mass or carcass mass was taken from 224 calves. We determined the age of all individuals by the time elapsed since they were radio-collared as calves or in the laboratory by counting the number of layers in the secondary dentine of the incisors (Haagenrud 1978) after the individual was harvested or found dead. To determine calving date and the number of calves produced, radio-collared females were approached on foot during the calving season (May–July) at 3 to 5-day intervals until the presence of one or two calves was verified (Sæther et al. 2003). We determined the age of calves when observed by their size and behaviour, as well as the physical condition of their mother (Sæther et al. 2003). The same procedure was repeated in autumn just prior to the hunting season (late September) to determine loss of calves during summer. By this procedure, we were able to determine the date of calving within ±1 day, as well as litter size per female just after calving and litter size per female in the autumn, approximately at the time of weaning.

Climate and population density

Climate data from Vega were provided by the Norwegian Meteorological Institute, Oslo, Norway (www.met.no). Based on monthly mean values, we calculated the annual variation in mean winter (November–April) temperature

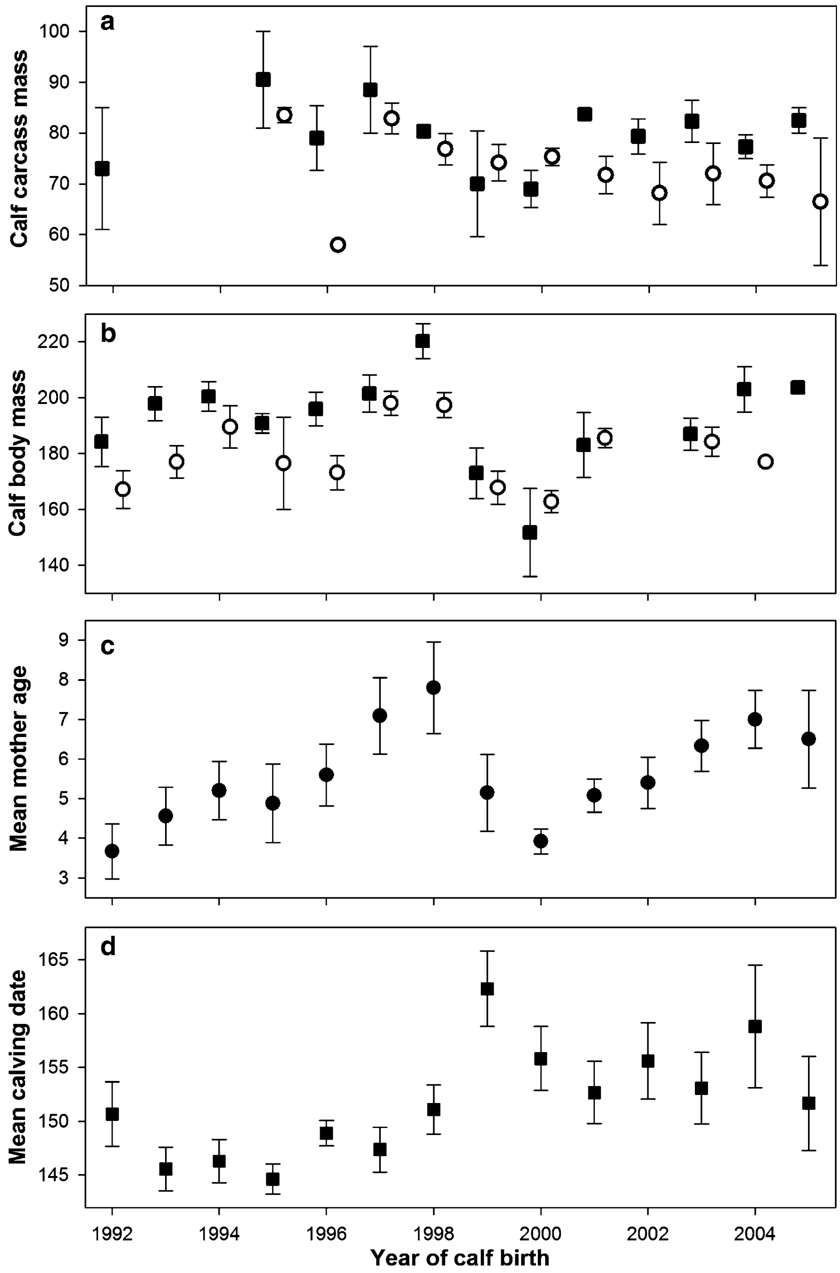

Fig. 2 Annual variation in **a** mean calf carcass mass (kg, females *circles*, males *squares*, ±1 SE), **b** mean calf body mass (kg, females *circles*, males *squares*, ±1 SE), **c** mean mother age (±1 SE) and **d** mean calving date (±1 SE) at Vega during the period 1992–2005. Calving date is measured as days after January 1st

($\bar{x} = 1.9$°C, CV = 40.6%), mean winter snow depth ($\bar{x} = 4.9$ cm, CV = 116.8%), mean winter precipitation ($\bar{x} = 119.8$ mm, CV = 24.8%), mean winter wind speed ($\bar{x} = 7.6$ m/s, CV = 12.2%), winter length (number of months with snow > 5 cm, $\bar{x} = 2.0$ months, CV = 78.5%), mean early summer (May–June) temperature ($\bar{x} = 9.2$°C, CV = 14.4%), mean late summer (July–August) temperature ($\bar{x} = 13.3$°C, CV = 9.9%), mean early summer precipitation ($\bar{x} = 67.2$ mm, CV = 33.9%) and mean late summer precipitation ($\bar{x} = 75.9$ mm, CV = 29.8%). We then performed two principal component analyses based on either winter or summer climate to reduce the number of variables. Two principal components were estimated (eigenvalues, % variance explained = 2.46, 49.2 and 1.75, 35.0, respectively) based on the winter variables (winter PC1 and PC2) and one component (1.22, 61.1) based on the summer variables (summer PC1). Winter PC1 was mainly influenced by temperature ($r = 0.91$), precipitation ($r = 0.75$) and snow depth ($r = -0.77$) while winter PC2 was mainly influenced by winter length ($r = 0.75$) and wind speed ($r = 0.81$). Summer PC1 was negatively related to temperature in early ($r = -0.63$) and late summer ($r = -0.90$) and positively related to precipitation (early: $r = 0.77$, late: $r = 0.79$). We also tested the effect of the North Atlantic Oscillation winter index (NAO, Hurrell 1995) on calf body mass. The NAO for the study period was retrieved from: www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naostatdjfm.

Winter population density was estimated based on the number of radiocollared moose present on the island, the number of calves in company with collared females, and other non-collared moose observed during periods of winter captures or by our locally employed research technician. The high number of radio-collared moose, small spatial scale, open landscape and frequent surveys by helicopter during marking operations ensures that the population size can be estimated with high accuracy. During the study period, the estimated population density ranged between 0.31 (1992) and 0.54 (1994) moose per km^2 inhabitable moose habitat ($\bar{x} = 0.41$, CV = 15.6%).

Analyses

We first logarithm-transformed the calf body masses to control for the different variances among calves measured in autumn (carcass mass) and winter (live body mass, Fig. 2a, b). We then analysed the contributions of the different explanatory variables on (ln) calf body mass by applying linear mixed effect models to the data (lme procedure in R, R Development Core Team 2006). Mother identity was included as a random factor (random intercept) to account for the interdependence due to several calves within each mother. We tested if variation in calf body mass was affected by variation in calf sex, litter size, calf age, calving date and mother age as fixed effects. Calf age indicates whether the calf was weighted in autumn or in winter (Fig. 2a, b). We also included the interaction calf age × weighing date in the model to account for a slight increase in carcass mass with weighing date in autumn ($r = 0.13$, $n = 96$, $P = 0.28$) and slight decrease in live body mass over time in winter ($r = –0.18$, $n = 128$, $P = 0.15$). The effects of litter size (1 or 2 calves) were tested based on litter size in spring or litter size at weaning (late September). Twelve twin litters recorded in spring were reduced to single calf litters by the autumn. Because competition for resources between siblings may occur both during foetus development and during the suckling period, we predicted that litter size in the autumn had the strongest effect on calf body mass.

We also included the effect of calving date and mother age as quadratic terms to account for possible nonlinear relationships. Similarly, we tested for two-way interactions including calf sex, litter size, calf age, calving date and mother age. We expected male calves to be more affected by mother age and calving date than female calves as male calves are commonly found to be more motivated to suckle (e.g. Festa-Bianchet 1988; Birgersson et al. 1998) and grow faster (e.g. Loison et al. 2004; Garel et al. 2006) than female calves (Isaac 2005). Moreover, we predicted that the effects of mother age and calving date on calf body mass should be less pronounced among calves weighed in winter (age 8 months) than in autumn (age 4 months) as calves become less dependent on their mother as time proceeds (Clutton-Brock 1991). We had no specific predictions regarding the other interactions.

To provide a baseline against which we could compare the more complex models, we estimated the variance components in a model with mother identity included as random factor and calf age and intercept included as fixed factors. We controlled for calf age in the baseline model because most of the difference in mass between autumn and winter was due to body mass in autumn being measured as carcass mass (i.e. about half of the live body mass, Fig. 2a, b) and not because of body growth. Two variance components were extracted from this model, representing the variances in calf body mass that are attributed to variation between mothers and within mothers (residual variance). Based on this model we (1) determined to what extent mean calf body mass varied between mothers (and therefore require a multilevel approach) and (2) estimated the fraction of explainable variation accounted for by the fixed effects in the more complex models. Following Singer (1998), we computed the proportion explainable variation explained as: (VC1–VC2)/VC1, where VC1 and VC2 are the variance components in the baseline and the more complex model, respectively.

Because we were particularly interested in what factors that best explained the annual variation in calf body mass, we also performed a second analysis where we tested the relationship between (ln) calf body mass and the variation in annual means of mother age, calving date, calf sex, litter size, as well as the effects of annual variation in climate and density. As above, we included calf age (as factor) and weighing date to control for the variation in calf mass over time within and between seasons (autumn, winter). Because of relatively large annual variation in mother age and calving date (Fig. 2c, d), we expected these variables to also explain a large part of the annual variation in calf body mass (Fig. 2a, b). In contrast, we expected small effects of varying winter climate on calf body mass given the mild winters, low-snow depth and therefore easy access to plants in the field layer. However, relatively strong winds combined with high precipitation as rain during winters can potentially induce thermoregulatory costs on the mother that are subsequently transferred to the calf/calves (e.g. Clutton-Brock et al. 1982). Similarly, smaller calves were expected after warm and wet summers (e.g. Sæther 1985; Solberg and Sæther 1994) because of negative effects on digestibility and nutritional quality of plants utilised by moose during the green season (Garel et al. 2006). No strong density-dependent effects were expected

Table 1 The results of the mixed effect models analysing the variation in moose calf body mass

Model	Weighing date	Calf age	Mother age	Calving date	Calving date^2	Litter size	Calf sex	Calf age × weighing date	Mother age × calf sex
BM		X							
1	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	
2	X	X	X	X	X	X	X	X	
3	X	X	X	X	X	X	X	X	X
4	X	X	X	X	X	X	X	X	
5	X	X	X	X	X	X	X	X	X
6	X	X	X	X	X	X	X	X	X
7	X	X	X	X	X	X	X	X	
8	X	X	X	X	X	X	X	X	
9	X	X	X	X	X	X	X	X	
10	X	X	X	X	X	X	X	X	
11	X	X	X	X	X	X	X	X	X
12	X	X	X	X	X	X	X	X	
13	X	X	X	X	X	X	X	X	
14	X	X	X	X	X	X	X	X	
15	X	X	X	X	X	X	X	X	
16	X	X	X	X	X	X	X	X	
17	X	X	X	X	X	X	X	X	X
18	X	X	X	X	X	X	X	X	
19	X	X	X	X	X	X	X	X	
20	X	X	X	X	X	X	X	X	X
21	X	X	X	X	X	X	X	X	X
22	X	X	X	X	X	X	X	X	
23	X	X	X	X	X	X	X	X	X
24	X	X	X	X	X	X	X	X	X
25	X	X	X	X	X	X	X	X	X
26	X	X	X	X	X	X	X	X	
27	X	X	X	X	X	X	X	X	
28	X	X	X	X	X	X	X	X	
29	X	X	X	X	X	X	X	X	
30	X	X	X	X	X	X	X	X	

Table 1 continued

Model	Mother age × calf age	Calf sex × litter size	Calving date × calf sex	Calving date × calf age	Calf sex × calf age	Litter size × calf age	Litter size × calving date	Calving date × mother age	Within mother variance	Between mother variance	ΔAICc
BM									0.01606	0.00350	100.70
1									**0.00985**	**0.00226**	**0.00**
2			X						0.00984	0.00213	0.05
3									0.00981	0.00223	0.10
4			X	X					0.00977	0.00221	0.34
5			X						0.00982	0.00211	0.53
6			X	X					0.00974	0.00219	0.79
7						X			0.00983	0.00228	0.89
8			X	X		X			0.00973	0.00224	0.97
9				X					0.00981	0.00235	1.00
10	X		X	X					0.00973	0.00224	1.01
11				X					0.00976	0.00232	1.02
12	X		X						0.00983	0.00215	1.11
13			X			X			0.00984	0.00214	1.17
14	X								0.00983	0.00230	1.21
15							X		0.00980	0.00242	1.38
16				X		X			0.00975	0.00239	1.44
17	X								0.00980	0.00227	1.47
18			X		X				0.00982	0.00223	1.55
19								X	0.00989	0.00221	1.60
20	X		X	X					0.00971	0.00223	1.66
21						X			0.00982	0.00225	1.67
22			X	X	X				0.00973	0.00232	1.74
23	X		X						0.00980	0.00214	1.76
24								X	0.00985	0.00218	1.83
25							X		0.00979	0.00236	1.88
26			X				X		0.00983	0.00223	1.92
27	X		X	X		X			0.00970	0.00227	1.94
28					X				0.00985	0.00234	1.94
29		X	X						0.00988	0.00212	1.97
30	X			X					0.00978	0.00239	1.97

X indicates variable included in the model. Litter size is litter size as observed in the autumn. BM is the baseline model with only mother identity as random factor (intercept) and calf age as fixed factor (AICc = –255.9). Models 1–30 are the models with the best combination of available explanatory variables (ΔAICc ≤2). Within and between mother variance are the variance components after including fixed effects. ΔAICc indicates the difference in AICc between the selected best (model 1, bold: AICc = –356.6) and alternative good models on calf body mass given the generally low-moose density, mild winters and easy access to agricultural fields on the island.

We considered the models with the lowest Akaike information criterion (AIC) score to be the most parsimonious and thus the 'best' model applied to the data (Burnham and Anderson 1998). We used AICc (corrected AIC) rather than AIC as we had a high number of parameters in relation to sample size (Burnham and Anderson 1998). Models that differed in AICc (absolute value) by two or less (ΔAICc ≤2) were considered to have the same support by the data (for a general discussion of AIC see Burnham and Anderson 1998). In the mixed effect models, parameters for fixed effects were estimated using Restricted Maximum Likelihood (REML). However, because we compared models with different fixed effect structure, we used Maximum-Likelihood (ML) for model selection (Singer 1998; Crawley 2002). All statistics were performed using SPSS 14.0 for Windows (SPSS 2005) and R 2.4.0 for Linux (R Development Core Team 2006).

Results

Body mass was measured in 224 moose calves distributed on 32 mothers in the period 1992–2005. On average, seven calves were measured for each mother, ranging from 1 ($n = 3$) to 13 ($n = 3$). Calf body mass (ln) varied significantly between mothers ($F_{31,189} = 2.68$, $P < 0.001$, controlling for calf age, weighing date and the interaction calf age × weighing date), although the variance component was more than four times higher within (0.01606) than between mothers (0.00350, Table 1). However, by estimating the intraclass correlation (Singer 1998), $r = 0.00350/(0.00350 + 0.01606) = 0.18$, we see that there was quite some clustering of calf body mass within mothers, justifying the use of mixed effect models.

Variation in calf body mass in relation to mother age, calving date, calf sex, age and litter size

Variation in calf body mass was best explained by the effects of mother age, calving date, calf sex, litter size, calf age and weighing date (model 1, Table 1). The litter size in autumn was in all models explaining more variation in calf body mass than litter size at birth. Calf body mass was larger for males than for females, larger for single than twin calves, decreased with increasing calving date and increased with mother age (Table 2, Fig. 3). A stronger decrease in calf body mass was evident towards the end of the calving season (significant quadratic calving date, Table 2, Fig. 3a), but we found no indications that being born very early in the season had negative effects on calf body mass (Fig. 3a). We verified the significance of the quadratic calving date effect by a randomisation test (i.e. by resampling calving date 10,000 times, $P = 0.007$, Crawley 2002). Furthermore, the effect of weighing date on calf body mass varied with calf age (interaction weighing date × calf age, Table 2), which was expected given the increase in body mass with time in autumn and decrease with time in winter (Methods).

Table 2 Parameter estimates and test statistics for the best mixed effect model (model 1, Table 1) explaining the variation in (ln) calf body mass of moose on Vega

Variables included	β	±SE	t	P
Intercept	–0.3828	1.3512	–0.283	0.777
Weighing date	0.0070	0.0020	3.534	<0.001
Calf age	2.9037	0.5681	5.111	<0.001
Mother age	0.0187	0.0032	5.760	<0.001
Calving date	0.0386	0.0144	2.674	0.008
(Calving date)^2	–0.0001	0.0000	–3.121	0.002
Litter size	–0.0422	0.0170	–2.484	0.014
Calf sex	0.0684	0.0140	4.878	<0.001
Calf age × weighing date	–0.0073	0.0021	–3.559	<0.001

The parameter estimates (β) for calf sex, calf age and interaction calf age × weighing date are associated with the factor level male, winter and winter, respectively (i.e. males and calves weighed in autumn kept constant)

The best model accounted for about 39 and 35% of the variation in calf body mass within and between mothers, respectively (Table 1). Testing the separate effects of mother age and calving date, while controlling for calf age and weighing date, indicated that both variables explained some variation in calf body mass within (mother age: 10%, calving date: 21%) and between mothers (mother age: 15%, calving date: 43%). The latter was probably due to the variation in mean age ($F_{31,192} = 6.35$, $P < 0.001$) and calving date ($F_{31,192} = 5.72$, $P < 0.001$) between mothers.

Another 21 models were within ΔAICc ≤2 from the selected best model (Table 1). These models included all the main effects from the selected best model, but included different interaction terms. There were some indications that the negative effect of calving date on calf body mass was stronger for calves measured in autumn than in winter (interaction calving date × calf age, $P > 0.131$, Table 1). Similarly, we found some indications for an interaction between mother age and calf sex ($P > 0.146$) and between calving date and calf sex ($P > 0.081$, Table 1). In all cases, mother age had stronger positive effect (steeper slope), whereas calving date had stronger negative effect on male than female calf body mass. Hence, male calves seem to be more sensitive to variation in maternal traits than are female calves.

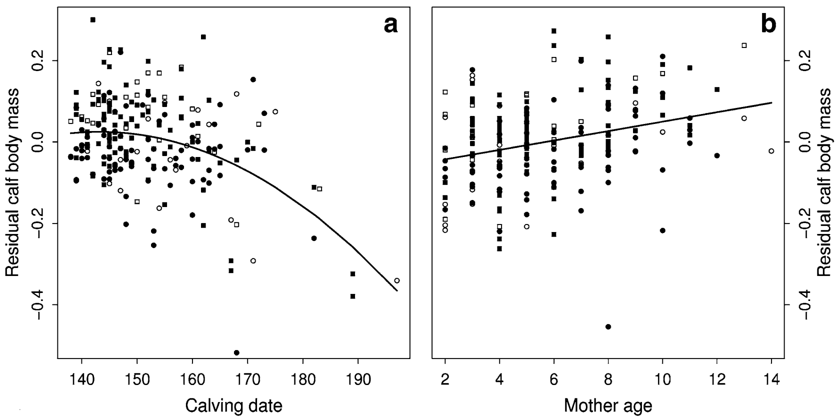

Fig. 3 Residual calf body mass in relation to **a** calving date and **b** mother age of moose on Vega during the period 1992–2005. *Open* and *closed* symbols indicate single and twin calves, while *circles* and *squares* indicate female and male calves, respectively. Calving date is measured as days after January 1st. The relationships are based on the best model (model 1, Table 1), controlling for other effects

Variation in calf body mass in relation to year of birth, density and climate

The annual variation in (ln) calf body mass was best explained by variation in annual means of mother age and calving date, while controlling for calf age and the interaction calf age × weighing date (Table 3). As expected, the body masses of calves were higher in years with older mothers (β = 0.032, SE = 0.007, $P < 0.001$) and earlier calving (β = –0.008, SE = 0.002, $P < 0.001$). The effects of annual variation in calf sex and litter size were less important, and the same was true for density and climate (Table 3). In the different alternative models, years with higher calf body masses were associated with higher densities, higher NAO (mild and wet winters), lower summer PC1 (warm and dry summers), lower winter PC1 (cold, dry and snow-rich winters) and higher winter PC2 (long and windy winters), but the effects were never significant ($P > 0.335$). Moreover, neither of the models that included climate nor density explained substantial more of the variance within mother than model 1 (Table 3). In a linear model (GLM-Univariate, SPSS), the annual means of mother age and calving date in combination with weighing date explained 12 and 29% of the variation in calf body mass in autumn and winter, respectively. This was about 71–75% of the variance explained by year of birth (as factor) in combination with weighing date (autumn: R^2 = 0.16, winter: R^2 = 0.41). Hence, most of the annual variation in calf body mass in autumn and winter seemed to be caused by annual variation in female age structure and timing of the calving season, leaving little additional variation left to be explained by climate or density effects. Indirect effects of climate and density may however have influenced on calf body mass through the mother condition and its effects on calving date and calf growth. Examining the correlations between calving date and climate or density, we found that winter PC2 gave the best fit (earlier calving after long and windy winters), although not significantly (r = –0.340, n = 14, P = 0.235).

Discussion

A large proportion of the variation in body mass of moose calves over a 14 years period on Vega was explained by the variation in mother age, calving date, calf sex and litter size (Tables 1, 2). Because the mother age structure and calving date of mothers also differed among years, both variables were responsible for a large part of the annual variation in calf mass. In contrast, environmental variables and density, which are often found to generate cohort effects (e.g. Gaillard et al. 2003), were not dedicated any strong effects on calf body mass in the Vega population, despite quite large annual variation.

The positive effect of mother age on offspring size has been shown in a number of mammal species (e.g. Bernardo 1996; Loison et al. 2004), and may be related to an age-specific increase in body mass and condition of the mother (Sæther and Haagenrud 1985; Solberg and Sæther 1994). Large size is often correlated with high phenotypic quality (Gaillard et al. 2000b; Hewison and Gaillard 2001), and larger mothers therefore can allocate more resources to offspring than smaller mothers (e.g. Loison and Strand 2005). In reindeer *Rangifer tarandus* L., Skogland (1984) found a strong correlation between mother size and foetus size, and birth weight was positively associated with the body mass of the mother in red deer *Cervus elaphus* L. (Clutton-Brock et al. 1988), dall sheep *Ovis dalli* N. (Festa-Bianchet et al. 2000) and fallow deer, *Dama dama* L. (Pelabon 1997). Similarly, Keech et al. (2000) found that moose females with large rump fat thickness gave birth to larger calves in Alaska. Calf body mass may also depend on the quantity and quality of milk produced by the mother, which in turn depends on mother qualities such as age and body mass (Landete-Castillejos et al. 2005).

The calf body mass increased with mother age even after their mothers reached prime size. On Vega, body mass of females peak at about 6 years of age (Sæther et al. 2001), but no such asymptotic relationship existed between calf body mass and mother age (Fig. 3b). Possibly this is

Table 3 The results of mixed effect models analysing the annual variation in moose calf body mass

Model	Weighing date	Calf age	Annual mean mother age	Annual mean calving date	Annual mean calf sex	Annual mean litter size	NAO	Population density	Winter PC1	Winter PC2	Summer PC1	Calf age × weighing date	Within mother variance	Between mother variance	ΔAICc
BM		X											0.01606	0.00350	29.50
1	X	X	X	X								X	**0.01402**	**0.00248**	**0.00**
2		X	X	X									0.01434	0.00221	0.68
3	X	X	X	X						X		X	0.01399	0.00256	1.24
4	X	X	X	X				X				X	0.01398	0.00259	1.29
5	X	X	X	X			X					X	0.01407	0.00241	1.41
6		X	X	X			X						0.01435	0.00215	1.47
7	X	X	X	X		X						X	0.01407	0.00245	1.65
8		X	X	X				X					0.01428	0.00234	1.70
9	X	X	X	X							X	X	0.01407	0.00248	1.83
10		X	X	X		X							0.01436	0.00219	1.87
11	X	X	X	X					X			X	0.01407	0.00249	1.90
12	X	X	X	X			X			X		X	0.01399	0.00249	1.93

X indicates variable included in the model. Mean litter size is litter size as observed in the autumn. BM is the baseline model with mother identity included as random factor (intercept) and calf age included as fixed effect (AICc = −255.9). Models 1–12 are the models with the best combination of available explanatory variables (ΔAICc ≤2). Within and between mother variances are the variance components after including fixed effects. ΔAICc indicates the difference in AICc between the best model (model 1, bold: AICc = −285.4) and alternative good models

because older females more often produce single than twin calves, and therefore are able to produce larger than average calves for a given body mass. In general, twin calves are smaller than single calves in moose (e.g. Sæther and Heim 1993; Ericsson et al. 2001), and the proportion reproducing females that gave birth to twins decreased from about 80% at the age of five to less than 20% at the age of 12–15 years on Vega (Sæther et al. 2001). However, even when controlling for litter size in the model (Table 2) we found no asymptotic relationship between calf body mass and mother age (Fig. 3b), indicating that older females have more body reserves available to invest in each of the calves they produce. This may be due to some older females having better access to high quality food resources (e.g. Wolf et al. 1998; Gaillard et al. 1998) or are willing to allocate more resources to reproduction than younger females (Clutton-Brock 1984). The latter mechanism was suggested to account for the larger calves produced by the oldest females in a Swedish moose population (Ericsson et al. 2001), and similarly, Clutton-Brock (1984) found the reproductive effort in red deer females to increase with age, even after prime age was reached. Recently, Mysterud et al. (2005) found the same pattern to be present in male moose, indicating that terminal investment in reproduction (*sensu* Clutton-Brock 1984) is a general phenomenon in moose.

As predicted, individual variation in calving date also affected the variation in calf body mass on Vega. Late born calves were smaller in autumn and winter than early born calves, and this effect seemed to be stronger for those born in the end of the season than in the start (a significant quadratic term, Table 2, Fig. 3a). Early born calves may benefit by having a longer period of the vegetation growing season available for body growth and may take advantage of the particular high quality of emerging food plants in spring (Klein 1970; Bunnell 1982; Rutberg 1987; Skogland 1989; Albon and Langvatn 1992). Similarly, there was variation in mean calving date between mothers on the island, indicating that part of the calving date effect can be attributed to a mother effect, e.g. some mothers may ovulate and breed systematically earlier in the autumn than others (e.g. Bon et al. 1993 for mouflon, *Ovis musimon* P.) or their gestation period may on average be shorter (Kiltie 1982). Data on Alaska moose indicate that variation in female body condition can affect the gestation period (Schwartz and Hundertmark 1993; see Berger 1992 for Bison, *Bison bison* L.), and a similar mechanism may explain the variation in calving dates among females on Vega. To some extent this assumption is supported by the fact that primipareous (2, 3-year olds), and therefore smaller females, were found to give birth significantly later than pluripareous females on Vega (Sæther et al. 2001, 2003).

Based on previous studies, we were particularly interested in the potential influence of climate and population density on the variation in calf body mass between years (e.g. Sæther 1985; Solberg et al. 1999, 2004). A large proportion of the variation in calf body mass on Vega was due to annual variation (Fig. 2a, b), but most of the among-year variation was explained by variation in maternal age and calving date (Table 3). This was probably partly due to the large variation in female age structure and calving date on the island following the strongly sex- and age-biased harvesting during the 1990s (Methods, Sæther et al. 2003). Given the significant climatic effects on moose body mass reported in other populations (e.g. Herfindal et al. 2006), it was nevertheless surprising that neither of the remaining annual variation in calf mass could be explained by environmental variation or variation in density. However, despite an almost doubling of the population size during the study period (Sæther et al. 2007), the density of moose is still quite low on Vega (see e.g. Garel et al. 2006), allowing the moose access to high-quality food even during winter. Moose on the island may therefore be less dependent on high-quality food during summer for compensating their winter losses, which make them better able to retain a stable body condition over years (e.g. Sæther and Gravem 1988; Cederlund et al. 1991). This is in accordance with studies showing less environmental effects in populations not yet weakened by density dependence (Sæther 1997; Hallet et al. 2004; see Solberg et al. 2001 for reindeer, Coulson et al. 2001 for Soay sheep, *Ovis aries* L., Portier et al. 1998 for Bighorn, *Ovis canadensis* S.), and also concurs with Herfindal et al. (2006) that found temporal variation in calf body mass to be less affected by temporal environmental variation in high performance (measured as high mean body mass) than in low performance moose populations (low mean body mass). Thus, the moose may be conservative in exploiting temporary varying conditions for body growth when living under favourable conditions or perhaps the variation in body growth is increasingly more restricted by the physiological ceiling for the species as living conditions improve.

Considering the large annual variation in calf body mass observed on Vega (Fig. 2a, b), it is likely that variation in maternal effects such as mother age and calving date may also affect demographic traits and induce time lags in the dynamics in this population. Smaller calves are more likely to die during severe winters (Loison et al. 1999) and may mature at a later age. In addition, maternal effects can be transferred between several generations, generating delayed life-history effects (*sensu* Beckerman et al. 2002). In red deer, for instance, cohorts with low birth weights produce offspring with low-birth weights (Albon et al. 1987), indicating that previous environmental variation may have long-lasting effects. Theoretical studies have shown that such age-specific variation in demography strongly affects the population dynamics (Engen et al. 2007), independent of the current population density.

Whether similar delayed life-history effects occur in moose may depend on the level of compensatory growth from calf to adult and to what extent adult size affects litter size, calf mass or both. The level of compensatory growth from juvenile to adult stages seems to be low in most ungulates (Gaillard et al. 2003), and similar results are indicated for moose (Solberg et al. 2004). A small calf may therefore become a smaller than average adult female, which in turn may produce smaller calves. However, it may be adaptive for parents to avoid producing poor offspring (Lindström 1999), and because moose can produce both single and twin calves, smaller females (for their age) can also trade number for quality, and thus breaking the between-generation correlation in body mass. To better understand the potential for delayed life history effects in moose, future studies therefore should focus on the effects of maternal body condition, and not only age, on the body development of their offspring.

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