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POPULATION ECOLOGY - ORIGINAL PAPER

Lack of compensatory body growth in a high performance moose *Alces alces* population

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Abstract Considerable work has been done on disentangling important factors determining early development in body size, yet our knowledge of the extent to which animals living under varying conditions can achieve catch-up growth for a bad start in life is limited. Here, we investigated how body mass at the age of 8 months influenced adult body mass in a moose *Alces alces* population living under excellent environmental conditions on the island of Vega in northern Norway. We also investigated if mother age and birth date effects on calf body mass persisted until adulthood. We show that neither males nor females were able to show compensatory growth before they reached adulthood, and that part of the variation in adult body mass may have been due to variation in mother age and date of birth. The pattern observed in males can be related to their growth strategy in relation to reproduction, while such results were not expected in females where size-dependent start of reproduction is likely to interact with body growth. We suggest that the good environmental conditions experienced on Vega led to females having small somatic costs of an early start of reproduction or that larger females were able to acquire more resources for growth than their smaller conspecifics. In both cases, females that postpone their first reproduction may not be able to achieve catch-up growth for their lower early body mass compared to females that start reproduction at an early age. Our results concur with previous studies indicating that compensatory growth is weak in moose, increasing the likelihood that variation in life history characters are also transferred between generations.

Keywords Birth date · Catch-up growth · Mother age effects

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Introduction

Variations in several life history traits, such as survival and reproductive performance, are related to variation in adult body mass (Albon et al. 1987; Clutton-Brock et al. 1987; Loison et al. 1999; Gaillard et al. 2000b; McElligott et al. 2001; Veiberg et al. 2004), indicating that explorations of the sources of body mass variation can provide insight into mechanisms causing fitness variation between individuals. In ungulates, individual variation in adult body mass is often explained by variation in population density and climate (Sæther 1997; Gaillard et al. 1998), as well as by spatio-temporal variations in living conditions in early life (Post et al. 1997; Festa-Bianchet et al. 2000; Pettorelli et al. 2002). However, while several factors have been identified to have direct effects on body mass, variation in body mass may also reflect trade-offs between fitness components, such as growth and age of maturity, current and future reproduction and growth of parent and offspring (Stearns 1992; Sæther et al. 1996; Sand 1996; Langvatn et al. 2004; but see Roff and Fairbairn 2007). Accordingly, several long-term studies have shown that delayed effects of conditions in early life are widespread in ungulate populations (e.g. Albon et al. 1987; Skogland 1990; Post et al. 1997; Rose et al. 1998; Coltman et al. 1999; Forchhammer et al. 2001; Pettorelli et al. 2002; Gaillard et al. 2003), but sometimes with decreasing effect with increasing age (Solberg et al. 2004). In particular for long-lived species that grow during a large part of their life, reproduce several times and experience several years with varying environmental conditions, such trade-offs between fitness components may lead to compensatory growth, or catch-up growth, that may blur the effects of condition at birth on adult size (e.g. Toïgo et al. 1999).

For catch-up growth to occur, smaller young individuals would have to show higher absolute body growth over time than larger individuals (Hornick et al. 2000). This can happen if smaller or less developed individuals consume more food, more nutrient-rich food or otherwise are able to metabolise food more efficiently into body mass. In addition, individual- or sex-specific variation in growth strategies may be involved in this ability to compensate (e.g. Festa-Bianchet et al. 2000). Catch-up growth has often been observed in farm animals after periods with food restrictions (Hornick et al. 2000), and is also shown to occur in wild ungulates (e.g. white-tailed deer, *Odocoileus virginianus*, Cowan and Long 1962; red deer, *Cervus elaphus*, Suttie et al. 1983; bighorn sheep, *Ovis canadensis*, Festa-Bianchet et al. 1994, 2000; alpine ibex, *Capra ibex ibex*, Toïgo et al. 1999). The extent to which catch-up growth does occur may in turn depend on the severity of under-nutrition or malnutrition as well as the conditions under which animals are given the chance to recover, e.g. the level of food limitation (Hornick et al. 2000; Metcalfe and Monaghan 2001). Similarly, the stage of development is important for their ability to compensate; poor nutrition at earlier growth stages seems to be more severe for subsequent recovery than restrictions at growth-stages later in life (Wilson and Osborn 1960; Lindström 1999). In polygynous, sexually dimorphic species, males and females typically show different growth pattern and energy expenditure (Clutton-Brock et al. 1982, 1988), and thus may show different responses to varying conditions during early life (Festa-Bianchet et al. 1994, 2000; Toïgo et al. 1999). In red deer, male reproductive success is related to density-at-birth whereas female reproductive success is not (Kruuk et al. 1999). Similarly, Solberg et al. (2004) found that population density at birth accounted for a smaller proportion of the variation in adult body mass of females than of male moose, *Alces alces*. This suggests that males do not compensate to the same extent as females despite the fact that they often grow for a longer period (e.g. Garel et al. 2006), and thus potentially can have longer time to compensate for a poor start in life than females. Such different growth patterns between males and females can be a response to sexual selection, by which males are selected to grow as fast as possible to achieve high adult body mass and associated high reproductive success, whereas females are selected to trade growth for early sexual maturity and reproduction (Trivers 1972; Clutton-Brock et al. 1988). Depending on the variation in age at maturity, such costs of reproduction may therefore reduce the influence of early development on adult body mass of females (Festa-Bianchet et al. 2000). In American bison, *Bison bison*, heavier juvenile females matured earlier, but became smaller as adults than light juvenile females (Green and Rothstein 1991). A similar pattern may be hypothesised for moose, as the age at maturity may vary by several years depending on body mass (Sæther and Haagenrud 1983, 1985a; Sand 1996; M. Garel et al., in press), and costs of pregnancy and lactation on subsequent body growth may be substantial (e.g. Sand 1998; Schwartz 1998). Small juvenile moose females could therefore perform catch-up growth by postponing the first reproduction and as larger juveniles become as large as adults. Indeed, even smaller males could follow the same growth strategy by reducing their rutting activity at a young age (Solberg and Sæther 1994), since male body mass loss during the rutting season can be substantial (e.g. Schwartz 1998; Mysterud et al. 2005). However, based on the results from studies of body growth in sexually dimorphic ungulates, males appear to be less willing to change their energy allocation between growth and reproduction as compared to females (Festa-Bianchet et al. 2000, 2004; Bergeron et al. 2008).

In this paper, we examine how body mass among adult moose ($\geq$1 year old) varies according to their body mass as calves, and test to what extent (1) animals are able to compensate for a poor start, and (2) whether females show larger compensation in body growth than males. In particular, we were interested in doing this in a high performance population, as several recent studies indicate that the costs of reproduction may not be as explicit in populations not limited by food (e.g. Festa-Bianchet et al. 1998). In our study area, the island of Vega in northern Norway, winters are mild and moose have access to rich feeding grounds, including agricultural areas, year round (Sæther et al. 2003; Solberg et al. 2007). In addition, moose densities are kept low by harvesting (<0.5 moose per km^2), resulting in high specific population growth rates (Sæther et al. 2007). Consequently, the moose experience excellent conditions for body growth, which could reduce the somatic costs of early reproduction (Festa-Bianchet et al. 1998; Toïgo et al. 2002), and make compensational growth from juvenile to adults less likely. In contrast, abundant food (and/or high food quality) can also provide better conditions for compensatory growth to occur by giving small or late developed calves better opportunities for increasing food intake and catch-up growth before the age at maturity (e.g. Verme 1963; Albon et al. 1992).

Based on 101 moose calves that were captured, marked and weighed during 13 winters and later weighed as adults, we examined to what extent compensatory body growth occurred. In addition, we examined whether juvenile body mass was related to age at first reproduction, and whether date of birth and maternal age affected variation in adult body mass. In previous studies, we showed that calf body mass in autumn and winter was positively related to the age of their mother and negatively related to their date of birth (Sæther et al. 2004; Solberg et al. 2007). Hence, larger calves are usually born earlier in the season and by older than average mothers, but less is known about the extent to which these effects persist until adulthood.

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), approximately 100 km south of the Arctic Circle. The landscape is dominated by a mixture of agricultural areas, marsh, and moor land dominated by heather, *Calluna vulgaris*, and interspersed with small areas of deciduous forest and short-grown pine, *Pinus sylvestris*, forests. The deciduous forests are found mainly along rivers and creeks. The southwestern part of the island is more mountainous, with Trollvasstinden (800 m above sea level) as the highest point. The mountain area is very steep and not utilised by moose, leaving approximately 80 km^2 of the island as moose habitat. The climate is oceanic, with mild winters (November–April temperature, $\bar{x}$ = 1.9°C, range 0.63–3.10) and low snow cover (November–April snow depth, $\bar{x}$ = 4.9 cm, range 0–23.7) as compared to what it could be expected given the latitude. The summers are cool (June–August temperature, $\bar{x} = 12.5$°C, range

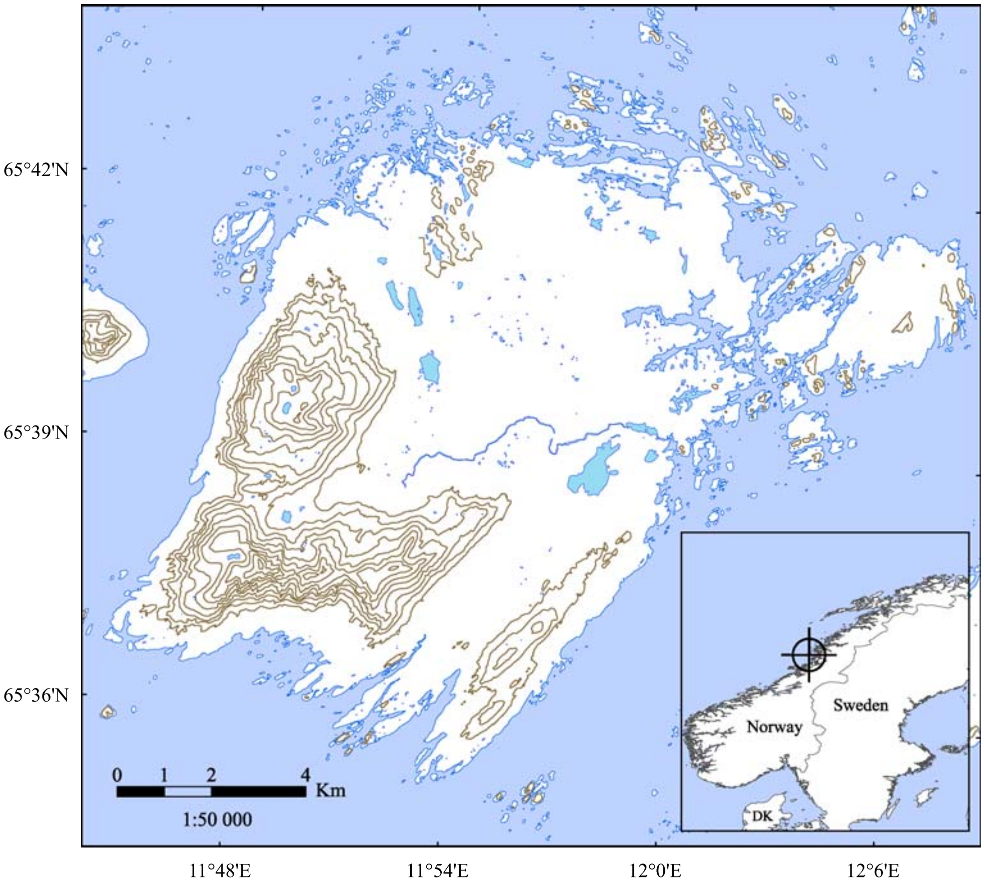

Fig. 1 The location of the study area, the island of Vega, Norway

10.8–15.4) and wet (June–August precipitation, $\bar{x} = 73.2$ mm, range 33.0–104.4).

The moose population

The study of the moose population at Vega was initiated in 1992 when 20 of 24 moose present on the island where captured, weighed and marked with radio-collars (Sæther et al. 2003). In the following years, we continued radio-marking new calves and immigrants to the island and changed collars on animals with malfunctioning radios. By this procedure, we were able to keep a large proportion (>90%) of the winter moose population marked. During the study period (1992–2005), 4–29 moose were harvested from the population each year, keeping the estimated winter population size within the range of 24–43 moose.

The study at Vega was initiated mainly to examine the effect of skewed adult sex ratios on fecundity and calving dates in a moose population (Sæther et al. 2003, 2004). To achieve this, the sex and age structures of the population were manipulated by selective harvesting during the period 1994–1999: In 1994, all adult (≥1.5 years) males in the population were killed after the rutting season, leaving only young (≤2.5 years) males as potential breeders in 1995 and 1996, but keeping a quite high adult sex ratio (c. 40% males). Thereafter, we reduced the adult sex ratio in the population to about 25% males from 1997 to 1999 while keeping some older males (≥4.5 years) in the population (Sæther et al. 2003, 2004). This manipulation was found to increase the mean calving date and subsequently decrease the body mass of calves and yearlings (Sæther et al. 2003; Solberg et al. 2007). To some extent, this manipulation may have increased the variation in body mass of calves by increasing the variation in calving date (Sæther et al. 2003; Solberg et al. 2007), but we have no reason to believe that the main results and conclusions of the present study are affected. For further information on the study site and moose population, see Sæther et al. (2003, 2004, 2007) and Solberg et al. (2007).

Data

When first captured (in January–March), all animals 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 for nearly all animals harvested during the autumn hunting season. Carcass mass is body mass after removing head, skin, metapodials, bleedable blood and viscera (Langvatn 1977). In a subsample of 22 moose ≥1 year old, we found carcass mass to increase linearly with total body mass just after death (i.e. an estimate of live body mass, both measures on log-scale) with a slope not different from one (isometric relationship; Fig. 2).

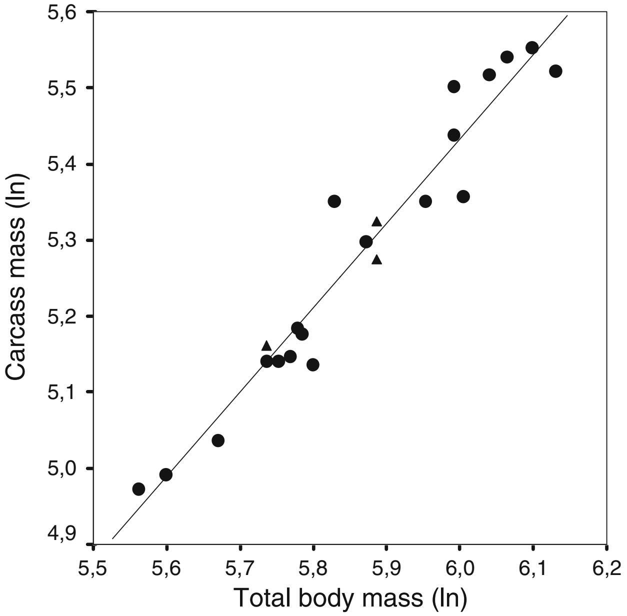

Fig. 2 Isometric relationship between log-transformed carcass mass (kg) and log-transformed total body mass (kg) in ≥1-year-old moose *Alces alces* on Vega (*circles* males, *triangles* females). The slope is estimated by linear regression ($b = 1.11$, 95% CI = 0.98–1.24, $n = 22$, $r^2 = 0.94$). Carcass mass represents about 56% of total body mass

During the study period 1992–2005, we used carcass mass data from 242 moose (108 females, 134 males) that were harvested during the autumn hunting season, and from which we have 101 live body mass measurements (42 females, 59 males) taken during winter at approximately 8 months of age. Another 3 adult (6–8 years old) males and 14 adult (4–8 years old) females that were weighed alive in winter 23 times (5 and 18 measurements for males and females, respectively) were also included. To account for the change in carcass mass during the hunting season (25 September–31 October), we adjusted the age- and sex-specific carcass masses for kill date. Similarly, we controlled for weighing date to account for a slight decrease in live body mass of moose captured during winter. Body mass was adjusted to 1 October and 15 February by using the slope of the linear regression between mass and kill date or weighing date, respectively (see, e.g. Herfindal et al. 2006).

We determined the age of all individuals used in the analyses by the time elapsed since they were radio-collared as calves or, for adults not collared as calves, in the laboratory by counting the number of layers in the secondary dentine of the incisors (Rolandsen et al. 2007). The incisors were collected from the animal after being harvested. Adult age was measured in years assuming that moose were born 1 June, killed 1 October and captured 15 February. Hence calves and yearlings killed during the hunting season were 0.33 and 1.33 years old, respectively, whereas calves measured in winter were 0.7 years old. The full value was used in estimation of growth models, whereas truncated age (e.g. 0, 1, 2) was used in the text.

For 94 calves with known winter body mass and for which we later obtained their carcass mass, we also possessed data on their date of birth and their mother's age. These calves were distributed on 28 mothers, ranging from 1 to 7 calves per mother. To determine birth date, radio-collared females were approached on foot during the calving season (May–July) at 3–5 day intervals until the presence of one or two calves was verified (see Sæther et al. 2003). Date of birth varied from 18 May to 2 July (45 days), and was measured as number of days since January 1.

Analyses

We first modelled the general body growth of males and females based on all available carcass masses ($n = 242$) collected during the study period to separate the growth phase and the mature phase when asymptotic carcass mass was reached (Fig. 3). Body growth was modelled using a monomolecular curve that account for a rapid initial growth followed by a levelling off without inflection point (France et al. 1996). This growth pattern is typical for precocious mammals (Gaillard et al. 1997b), and has also previously been used to model body growth in moose (Garel et al. 2006). The model can be described by the following equation:

$$M_t = \gamma - (\gamma - M_0)e^{-\beta t}, \qquad (1)$$

where M_t is carcass mass (in kg) at time t (in years, see above), γ is the asymptotic value, or adult carcass mass, M_0 is carcass mass at $t = 0$ (carcass mass at birth) and β is the decay in growth rate with age. Carcass mass at birth (M_0) was set to 6.5 kg, which is approximately 50% of live birth mass of moose in Norway (Andersen and Sæther 1996). We used 50% of birth mass because the carcass mass of calves at 4 months of age constitutes approximately 50% of live body mass (Wallin et al. 1996; see also Garel et al. 2006; Solberg et al. 2007; Fig. 2 and "Results"). Parameters were estimated using non-linear least-square estimation (Bates and Watts 1988). The length of the period with active body growth was estimated as the age when 99% of γ was achieved (Sand et al. 1995; Garel et al. 2006). We also computed confidence intervals (2.5 and 97.5% quantiles) of growth parameters by simulating 1,000 bootstrap replicates from the fitted model (Efron and Tibshirani 1993). We simulated new data by assuming, for a given sex j and age k, that an observation i is a random realisation of a normal distribution of mean μ_{jk} and standard deviation σ_{jk}. Data were simulated only when sample sizes were >1 for a given sex and age.

In the next step, we analysed the effects of sex, age and calf body mass ($n = 101$) on adult ($\geq$1 year old) body mass. Adult body mass was estimated based on the relationship between carcass mass and total body mass in Fig. 2, i.e. by dividing carcass mass on 0.56. To account for the age effect, we included all age groups within the period with active growth as indicated by the growth model (Fig. 3 and "Results"), as well as pooled age groups for older individuals in both sexes [females: 1 ($n = 24$), 2 ($n = 5$), 3 ($n = 3$), $\geq$ 4 (4–10 years, $n = 10$), males: 1 ($n = 38$), 2 ($n = 14$), 3 ($n = 4$), $\geq$6 (6–9 years, $n = 3$)]. In the absence of compensatory growth, we expected a positive relationship between calf body mass and adult body mass with a slope equal to or larger than one. Conversely, we concluded that smaller calves showed compensatory growth if the slope of the relationship between calf body mass and adult body mass was significantly less than 1. In effect, this means that smaller calves grow with a higher rate (e.g. body growth per year) than

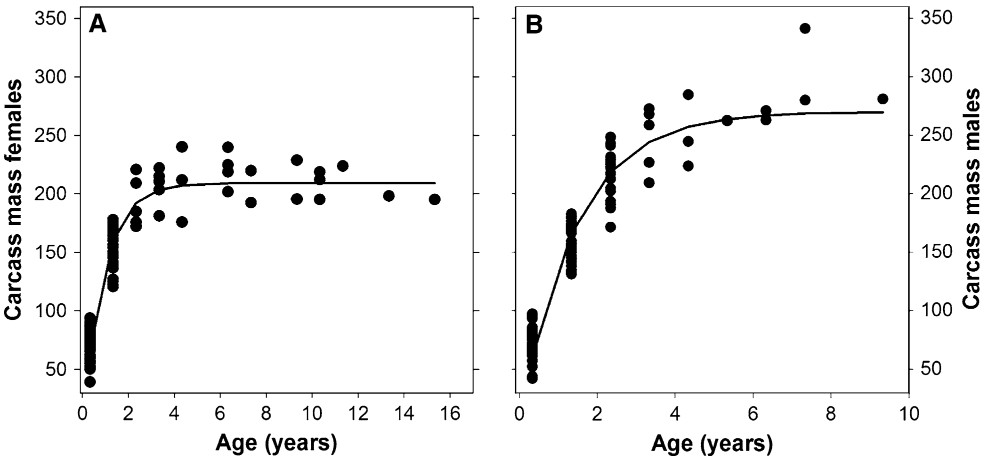

Fig. 3 Relationship between carcass mass (kg) and age (years) of females (**a**) and males (**b**) on Vega. Slopes are estimated by the equation $M_t = \gamma - (\gamma - M_0)e^{-\beta t}$, where Mt is carcass mass at time t, γ is the asymptotic value, M_0 is the carcass mass at $t = 0$ (at birth) and β is the decay in growth rate with age. See text for parameter estimates

larger calves. We also examined the effects of the two-way interaction between age and calf body mass to test for different responses in adult age classes, and between sex and calf body mass to test our prediction that females show more compensatory growth than males (see Toïgo et al. 1999; Festa-Bianchet et al. 2000), i.e. that the slope of the relationship between calf body mass and adult body mass is lower in females than in males.

We then tested if variation in calf body mass was related to the number of calves produced (0, 1 or 2 calves) at the age of 2 ($n = 21$) and 3 ($n = 9$). Unfortunately, we did not have enough data to examine whether body growth from calves to adults was affected by the number of calves they produced at the age of 2 or 3.

To examine to what extent the effects of maternal characteristics were lasting into adulthood, we tested the effects of mother age and birth date on the variation in adult carcass mass based on the restricted sample with information of mother characteristics ($n = 94$). We included the squared effect of birth date to account for a possible non-linear effect (see Solberg et al. 2007). In a second step, we included calf body mass to examine to what extent mother characteristics explained additional variation in adult body mass not already explained by calf body mass. We included all possible two-way interactions between sex or age and mother age, birth date and calf body mass.

We also analysed the effect of calf body mass, mother age and calving date on adult body mass for males (6–8 years old, $n = 5$ weights, $n = 3$) and females (4–8 years old, $n = 18$ weights, $n = 14$) in the restricted sample of animals weighed alive as adult. Because several animals were measured alive several times as adults, we included both identity and mother identity as random factors (intercept) in the model (see below). As above, we expected a positive effect of calf body mass and mothers' age on adult body mass and a negative effect of birth date.

We tested the above relationships using linear and linear mixed effect models (Univar and Mixed; SPSS 2007). In models including mother characteristics, we included mother identity as random intercept (Singer 1998) since several individuals were born by the same mothers. Mixed effects models are well suited to take care of such non-independence of errors by modelling the covariance structure introduced by the grouping of the data within mothers (Crawley 2002). For models based on the complete sample ($n = 101$), we did not include random mother effect as the identities of all mothers were not available.

To evaluate the alternative models for each set of data, we performed model selection using the Akaike information criterion (AIC; Burnham and Anderson 2002). We used AICc, rather than AIC, as sample size relative to the number of estimated parameters was relatively small (Burnham and Anderson 2002). This method (the information-theoretic approach) is not so much discriminating significant from insignificant factors, but rather decides which of many competing explanations is most consistent with the data, i.e. the best-fitted model for the data set (Burnham and Anderson 2002). For the sake of pluralism, we also report the effect size and precision of parameters and associated *P* values (Stephens et al. 2005), but *P* values were not used in the process of model selection (Anderson and Burnham 2002). Indeed, when using AICc for model selection also insignificant terms can be included in the best models if the effect size is large enough (evaluated by methods based on the Kullback–Leibler distance, Burnham and Anderson 2002).

We considered the models with the lowest AICc score to be the most parsimonious and therefore the best approximation for the information in the data (Burnham and Anderson 2002). Models for which differences in AICc (absolute value) were 2 or less ($\Delta\text{AICc} \leq 2$) have all substantial support (Burnham and Anderson 2002), and factors included in these models were therefore considered to be important for the variation in the response variable. In the mixed effect models, parameters for fixed effects were estimated using restricted maximum likelihood (REML), but 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 15.0.1 (SPSS 2007) or R 2.5.0 (R Development Core Team 2007).

Results

Body growth in male and female moose on Vega

Variation in carcass mass was to a large extent explained by variation in sex and age (Fig. 3; in females $r^2_{\text{adj}} = 0.94$, in males $r^2_{\text{adj}} = 0.92$). Males grew faster and for a longer time than females; 99% of asymptotic mass (γ) was reached at 6.5 years of age in males (95% CI 5.7–7.4) and at 4.3 years of age in females (95% CI 3.9–4.8). Accordingly, we pooled males $\geq$6.3 years of age ($n = 3$) and females $\geq$4.3 years of age ($n = 10$) into one age category in the subsequent analyses. The asymptotic carcass mass in autumn was 270 (95% CI 251.1–289.4) kg in males and 209 (95% CI 200.7–218.7) kg in females. Carcass mass constitutes about 56% of total body mass in autumn on Vega (Fig. 2), indicating that the asymptotic live body mass at 1 October is about 482 kg (270/0.56) in males and 373 kg (209/0.56) in females. For comparison, the mean body mass of $\geq$6.7-year-old males and $\geq$4.7-year-old females measured alive during winter (adjusted to 15 February) was 462 kg (95% CI = 434–490, $n = 5$ weights, $n = 3$ males) and 385 kg (95% CI = 368–402,

$n = 28$ weights, $n = 22$ females), respectively. Based on the mean values, the body masses of prime-aged males decreased from autumn to mid-winter while they increased in females. However, given the relatively wide confidence intervals these differences were far from significant ($P > 0.10$).

The relationship between calf and adult body mass

The variation in adult body mass was best explained by variation in calf body mass, age group and the two-way interaction calf body mass × age group (Table 1). The best alternative model also included an effect of sex (Table 1), but the sex-effect was not significant. This was probably due to the fact that only the three youngest age groups were common for both sexes, i.e. the ages prior to the development of strong dimorphism (Fig. 3). The two-way interaction calf body mass × age group was mainly due to the shallower slope for 3-year-old males and females (Fig. 4a, b, Table 3). The age-specific slopes for the relationship between calf mass and adult mass were significantly positive in yearlings and 2 year olds, but not significantly different from one in any age group (yearlings: $\beta = 0.86$, 95% CI = 0.53–1.19, 2 year olds: $\beta = 1.62$, 95% CI = 0.99–2.24, 3 year olds: $\beta = -0.42$, 95% CI = −3.02 to 2.18, ≥4 year olds: $\beta = 1.10$, 95% CI = −0.18 to 2.39; for sample sizes, see Fig. 4a, b; no separate slope was estimated for ≥6-year-old males because of the low sample size, $n = 3$). Including only data from prime-aged individuals (≥4 year olds and ≥6-year-old females and males, respectively) in the model (controlling for age) produced a common slope of $\beta = 1.31$, but given the low sample size ($n = 13$) this estimate was not significantly different from zero or one (95% CI −0.13 to 2.74). No models including a calf body mass × sex interaction were among the best models ($\Delta\text{AICc} \geq 2.72$; Table 1), and this term was never significant ($P > 0.47$). Hence, we found no support for our prediction that females showed larger compensatory body growth than males.

Reproduction in relation to body size as calf

There was significant variation in body mass as calf between females producing 0, 1 or 2 calves at the age of 2 ($F_{2,18} = 8.79$, $P = 0.002$). This was largely because females producing twins were heavier ($P < 0.05$) as calves ($\bar{x} = 202.9$ kg, SE = 3.8, $n = 4$) than those producing singletons ($\bar{x} = 170.2$ kg, SE = 4.2, $n = 8$) or no calf at all ($\bar{x} = 177.5$ kg, SE = 5.0, $n = 9$). A similar difference in body mass as calf was found among females producing twins ($\bar{x} = 191.2$ kg, SE = 9.8, $n = 3$) or singletons ($\bar{x} = 170.3$ kg, SE = 3.3, $n = 6$) at the age of 3 ($F_{1,7} = 7.31$, $P = 0.030$).

Table 1 Linear models explaining the variation in adult body mass of moose *Alces alces* ($n = 101$)

	Calf body mass	Age group	Sex	Age group × calf body mass	Sex × calf body mass	AICc	ΔAICc
M1	**X***	**X***		**X***		**966.04**	**0**
M2	X*	X*	X	X*		966.61	0.57
M3	X*	X*	X*			968.49	2.45
M4	X*	X*	X	X*	X	968.76	2.72

X indicates variable included in the model, X* being significant ($P \leq 0.05$). M1–M4 shows all models within ΔAICc < 3 of the best model. The selected best model was M1 (**bold**)

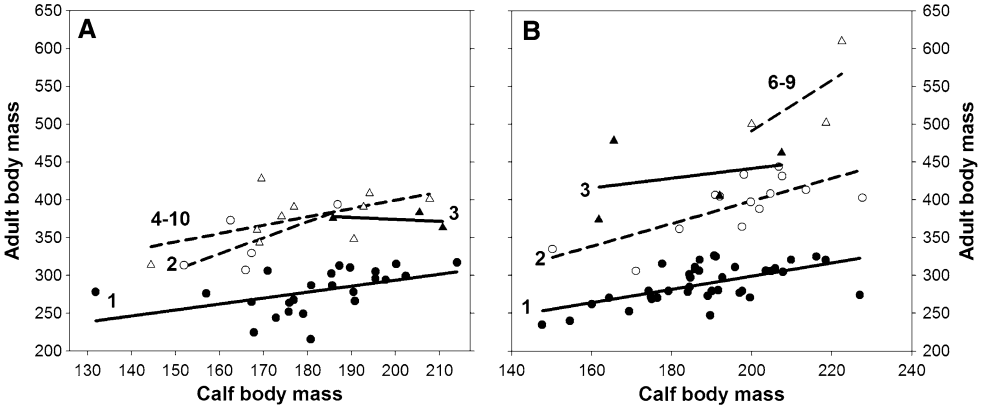

Fig. 4 Variation in adult body mass (kg) in relation to their body mass as calves for females (**a**) and males (**b**). *Numbers* in figure indicates age groups

Table 2 Mixed effect models explaining the variation in adult body mass using data on mother characteristics ($n = 94$)

	Mother age	Birth date	Birth date^2	Sex	Age group	Sex × birth date	Within mother variance	Between mother variance	AICc	ΔAICc
M1		**X**		**X***	**X***		**715.1**	**313.2**	**920.57**	**0**
M2	X	X		X*	X*		715.9	210.2	920.99	0.42
M3				X*	X*		715.2	352.8	921.02	0.45
M4	X			X*	X*		761.8	231.9	921.54	0.97
M5		X		X	X*	X	720.1	317.4	922.75	2.18
M6		X	X	X*	X*		723.2	316.4	923.04	2.47
M7	X	X		X	X*	X	760.0	214.6	923.27	2.70
M8	X	X	X	X*	X*		764.4	209.8	923.46	2.89

X indicates variable included in the model, X* being significant ($P \leq 0.05$). M1-M8 indicates all models within ΔAICc < 3 of the best model. The selected best model was M1 (**bold**). Birth date^2 is the square term of birth date. Within and between mother variances are the variance components after including fixed effects. In the baseline model, i.e. a model with fixed and random intercepts only (AICc = 1,053.15), the within and between variance components were 3,320.0 and 1,080.9, respectively

Adult body mass in relation to birth date and age of their mother

For the restricted sample of adult moose with known mother age and date of birth ($n = 94$), the variation in adult body mass was best explained by variation in birth date while controlling for sex and age group (Table 2). Alternative good models (ΔAICc ≤ 2) also included mother age or just sex and age group (Table 2). As expected, moose that were born late in the season or by younger mothers tended to be smaller as adults than moose that were born early (Table 3) or by older mothers ($\beta = 2.32$, 95% CI = −0.48 to 5.13). However, the effects were barely significant (e.g. birth date: $P = 0.087$, mother age $P = 0.104$). No model including an interaction term was among the best models (ΔAICc ≥ 2.18).

Because effects of birth date may depend on a few late born calves, we also tested models after excluding the four latest born calves (all born after 20 June) from the dataset. According to the AICc, all models (but one, M6) from Table 2 were still retained among the best models (i.e. ΔAICc < 3), but their order of priority changed to become: M4, M3, M2, M1, M8, M7 and M5. Hence, the best model now included the effect of mother age, sex and age group (similar structure as M4 in Table 2), whereas the second best model included only the effect of sex and age group (similar structure as M3 in Table 2, ΔAICc = 0.19). The best model including birth date (similar structure as M1 in Table 2) was slightly less supported (ΔAICc = 0.66), indicating that late born calves partly influence model selection based on the full sample ($n = 94$). However, as both mother age and birth date were present in several of the best models, and given the relatively low sample size, we suggest that both mother age and birth date should be considered potential causal factors for variation in adult body mass of moose.

Table 3 Parameter estimates and test statistics for the best models (M1) in Table 1 (A) and Table 2 (B)

Model	Variables	β	±SE	t	P
(A)	Intercept	−179.18	337.50	−0.53	0.597
	Calf body mass	3.35	1.58	2.12	0.036
	Yearlings	304.47	339.59	0.90	0.372
	2 year olds	254.04	342.05	0.74	0.460
	3 year olds	664.22	353.42	1.88	0.063
	4 year olds	357.65	349.21	1.02	0.308
	Calf body mass (yearlings)	−2.49	1.59	−1.57	0.121
	Calf body mass (2 years)	−1.73	1.60	−1.08	0.283
	Calf body mass (3 years)	−3.77	1.67	−2.26	0.026
	Calf body mass (≥4 years)	−2.25	1.65	−1.36	0.178
(B)	Intercept	614.67	59.50	10.33	<0.001
	Sex: females	−16.44	6.72	−2.45	0.013
	Yearlings	−229.02	17.10	−13.39	<0.001
	2 years old	−139.72	17.74	−7.87	<0.001
	3 years old	−130.33	25.29	−5.15	<0.001
	4 years old	−132.19	19.46	−6.79	<0.001
	Birth date	−0.65	0.39	−1.66	0.087

Mother identity is included as random factor (intercept) in model B. For the fixed factors, sex, age group and interaction calf mass × age group, males and ≥6 year olds are held constant

When testing for the effect of calf body mass in combination with mother characteristics on the restricted sample ($n = 94$), the best model included age group, calf body mass ($\beta = 3.35$, 95% CI = 0.61–6.09) and the interaction age group × calf body mass (AICc = 888.12; Table 2). As for the analyses based on the full sample ($n = 101$; Table 1), the interaction was mainly due to the more shallow relationship between body mass at the age of 3 and their body mass as calf (as indicated in Fig. 4 and Table 3 for the model based on the full sample). A model excluding the interaction age group × calf body mass gave almost the same fit (AICc = 888.42). Both models outperformed by far all models including only mother characteristics (ΔAICc ≤ -32.16). Given our previous findings that mother age and birth date had a strong impact on the variation in calf body mass at the age of 8 months (Solberg et al. 2007), these results indicate that mother effects on adult mass primarily work through the mother effects on calf mass.

Adult live body mass in relation to calf body mass, birth date and mother age

Based on the 17 adult moose that were weighed alive during winter ($n = 23$ measurements), and for which we also possessed their calf body mass, the best model (AICc = 227.76) included sex (females: $\beta = -46.99$, 95% CI = −92.30 to −1.17), calf body mass ($\beta = 2.10$, 95% CI = 0.88–3.31) and mother's age ($\beta = -6.09$, 95% CI = −12.21 to 0.02). However, contrary to expectations, the estimated effect of mother age was negative, probably due to the positive correlation between calf body mass and mother's age (Solberg et al. 2007). An alternative good model (ΔAICc = 1.33; Fig. 5) and the only other model within ΔAICc ≤ 2 from the best model, included sex (females: $\beta = -52.14$, 95% CI = −102.20 to −2.00) and calf body mass ($\beta = 1.26$, 95% CI = 0.30–2.23) without a mother age effect. In both models, the estimated slope indicated that smaller calves were not able to catch-up in body mass on larger calves before prime age (i.e. the 95% CI of the slope included one). Excluding calf body mass from the analyses produced models that were substantially less supported than models including calf body mass (ΔAICc ≥ 9.0).

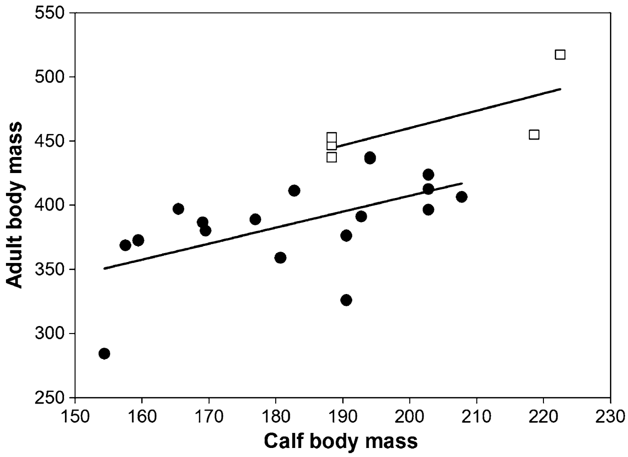

Fig. 5 Live body mass (kg) of adult (4–8 years old) females (*closed circles*) and adult (6–8 years old) males (*open squares*) in winter in relation to their winter body mass as calves

Discussion

In this study, we show that male and female moose follow different growth strategies (Fig. 3) and that variation in body mass of moose calves at approximately 8 months of age extends into adulthood (Fig. 4). Smaller calves were not able to grow with a higher rate than larger calves (Table 3), and although larger juvenile females produced more calves at the age of 2 and 3 (also see Sæther and Haagenrud 1983, 1985a; Sand 1996), we found no strong support for the hypothesis that varying start of first reproduction affected their subsequent growth (Fig. 5, Table 3). A similar effect was indicated for maternal characteristics, as date of birth and mother age were not only important for the variation in calf body mass at about 8 months of age (Solberg et al. 2007), but also affected the variation in adult body mass (Tables 2, 3). However, the support for an effect of birth date and/or mother age on adult body mass was rather weak, possibly because of the limited power of the statistical tests. Moreover, because of the small sample of old males included in the analyses, the lack of any compensatory growth from calves to prime age should be interpreted with caution.

Body growth in males and females

Body growth was faster in males than in females. In addition, the asymptotic mass was reached approximately 2 years later in males (Fig. 3). The asymptotic carcass mass in females was about 23% lower than in males, which is located within the range of sexual dimorphism for mainland populations in Norway ($\bar{x} = 24\%$; Garel et al. 2006). Still, the asymptotic body mass of Vega males is the highest reported from Norway (Garel et al. 2006, Appendix B), supporting the assumption that rich feeding condition and low population density allow moose to grow large in this population. This was also supported by the fact that the mean body mass of prime-aged males and females during winter did not differ significantly from the asymptotic mass recorded in autumn (but note the low test power and different estimations methods), which was not expected based on experiences from more food-constrained populations (Sæther and Haagenrud 1985b; Mysterud et al. 2005). Adult females usually gain weight during the entire autumn, then lose body mass during winter (Schwartz et al. 1987; Schwartz 1998). In contrast, adult males usually reach their peak body mass just prior to the rut—which on Vega is assumed to peak around 10 October (E.J. Solberg et al., unpublished data)—and lose weight during the rut due to high activity and cessation of eating (Miquelle 1990; Schwartz 1998). Accordingly, Mysterud et al. (2005) estimated the weight loss of adult males during rut to be 9–11% based on data from seven populations in Norway. Although part of this loss may be regained just after the rut, additional weight loss occurs before spring; the magnitude depending on length and severity of winter (e.g. 7–23% loss of pre-rut mass; Schwartz 1998). However, as judged from the few live weights of prime-aged males and females, there is no substantial weigh loss before mid-winter (15 February) at Vega, probably because the systematic lack of deep snow are not restricting the access to food in the field layer or increasing the energetic costs associated with moving.

No compensatory body growth

To compensate for the negative impact of delayed growth, organisms are predicted to have evolved compensatory strategies to minimise the fitness cost (Metcalfe and Monaghan 2001). Delayed growth may for instance predispose moose calves to higher overwinter mortality, as is observed for red deer (Clutton-Brock et al. 1987; Loison et al. 1999), increasing age at maturity (Sæther and Haagenrud 1983, 1985a; Sand 1996; Heard et al. 1997) and lower adult fertility (Sand 1996). In our study, late-developed moose calves were unable to compensate for the absolute differences in body mass they had developed by the age of 8 months. However, this may not exclude the possibility that some compensatory growth did occur prior to their first winter. For instance, in roe deer, *Capreolus capreolus*, Gaillard et al. (1997a) found that fawns were able to compensate for delayed early growth in a high performance population (see also Gaillard et al. 1993), whereas late born fawns in a low performance population were not. In support of the latter, Keech et al. (1999) did not find compensatory growth from birth to 10 months of age in a high density moose population in Alaska, possibly due to density dependent limitations in the amount of maternal investments in the calf (also see Cederlund et al. 1991).

Despite the high performance of the Vega population, however, we find it unlikely that calves performed any substantial catch-up growth during their first 8 months of life given the fact that mother age and calving date were important determinants of variation in winter body mass of calves (Solberg et al. 2007). Most calves are born during a 4-week period from mid-May, but some calving may occur as late as in the first week of July (Solberg et al. 2007). At this stage, early born calves may have tripled their birth weight (Schwartz 1998), which obviously gives them a strong advantage with respect to the absolute body mass they can attain before winter. Because larger calves in winter were born by older (and larger) than average mothers, they were probably larger at birth (see Ericsson et al. 2001) and possibly also nursed above average during summer (Solberg et al. 2007). This mechanism can provide calves born by older mothers with an additional benefit to the head start given by their larger birth weight. This was also supported by Keech et al. (1999), who showed that larger moose calves grew with a higher rate from birth to 10 months of age than smaller calves (see Schultz and Johnson 1995; Pélabon 1997, for similar results for white-tailed deer, and fallow deer, *Dama dama*, respectively). Thus, if anything, larger moose calves at birth appears to grow with a higher rather than lower rate than smaller individuals during their first season of growth.

Because pregnancy and successful rearing of offspring are expensive activities in mammals (Bell and Koufopanou 1986; Stearns 1992), we also expected compensatory growth between juvenile and mature age classes in females. Body growth has been found to be lower in moose females that successfully reared a calf until autumn (Sand 1996; Schwartz 1998) and—as in many other ungulates (e.g. Bauer 1987 in chamois *Rupicapra rupicapra*, Sadleir 1987 in cervids, Verme and Ozoga 1987 in white-tailed deer, Hewison 1996 in roe deer)—female body mass is associated with age at maturity in moose (Sæther and Haagenrud 1983; Sand 1996). Smaller females thus have the opportunity to grow by delaying age at first reproduction (e.g. Festa-Bianchet et al. 2000), whereas the larger females have to pay the energetic costs of reproduction, possibly at the expense of further somatic growth (e.g. Clutton-Brock et al. 1983; Festa-Bianchet et al. 1998). In support of this, Sand (1998) found moose females that nursed two calves during summer to have significantly smaller autumn body mass than females that did not reproduce or nursed only one calf until autumn (see also Sæther and Haagenrud 1985a; Testa 1998; Testa and Adams 1998). However, despite the significant effect of juvenile body mass on early reproduction also found on Vega, we did not find this to affect their subsequent growth.

Several mechanisms can potentially explain this lack of catch-up growth. First, young individuals that start to reproduce early may also experience higher early calf loss and subsequently no extra costs of nursing the calf during summer. The costs of reproduction are related to both foetus growth and lactation, where the nursing of calves during summer constitutes the highest costs (Sadleir 1969; Clutton-Brock 1991). However, the summer calf survival is in general very high on Vega (87–94%; Stubsjøen et al. 2000; Veisetaune 2003), and although there is a slight tendency for 2-3-year-old females to lose more calves during summer (summer survival of calves = 0.92) compared to prime-aged (4–11 years old) females (summer survival of calves = 0.92–1.00; Veisetaune 2003), this difference is hardly enough to explain the lack of compensatory growth in adult females.

Second, the lack of compensatory growth can be related to the sampling procedure. Because hunters preferably shoot adult females not in company with a calf/calves (e.g. Solberg et al. 1999, 2000; Nilsen and Solberg 2006), our sample of carcass masses may have been biased in favour of adult females that have not experienced the reproductive cost in the year of death. Examining the sample of hunter-killed adult females from which we had reproductive data from the same year ($n = 18$) supported this notion: only 20% of 2 year olds ($n = 5$) and 69% of older females were observed with calf/calves, whereas the corresponding figures in the population was about 56 and 95% for 2 year olds and older females, respectively (Sæther et al. 2001, 2004). Thus, there is a tendency for adult females to enter the hunting sample in years with reduced costs of calf rearing, possibly blurring the expected relationship between calf body mass and post-maturity female body mass. However, as the same relationship was found between calf body mass and their adult body mass when captured alive during winter (Fig. 5), we do not believe that sampling bias has caused the observed pattern.

A third, and more likely, explanation for the lack of catch-up growth among females is that the costs of calf rearing may not be as explicit in populations not limited by food (Clutton-Brock et al. 1983; Festa-Bianchet 1989, 1998; Stearns 1989; Toïgo et al. 2002) and that the cost is overruled by individual heterogeneity in the capacity to acquire resources (van Noordwijk and de Jong 1986). In ungulates, the life-time reproductive success of females is related to their life expectancy (Stearns 1992; Bérubé et al. 1999; Gaillard et al. 2000a; Weladji et al. 2006), and mothers may therefore only allocate surplus energy to reproduction as long as it is not compromising their own survival and reproductive value compared to that of their calves (Festa-Bianchet and Jorgenson 1998). For a juvenile female in good condition that starts to breed early, the necessary allocation of energy to successful calf production may therefore be relatively small compared to the resources that she has available for further growth, in particular in favourable environments. Moreover, as individuals do not only vary in the proportion resources they can allocate to reproduction, but also in the total amount of resources they can acquire, the expected trade-off may fail to appear if there is relatively large variation in the latter (van Noordwijk and de Jong 1986; Stearns 1992). Thus, if larger juvenile females can acquire more resources than their smaller conspecifics this may compensate for the costs associated with their earlier reproduction. Having no information on the individual variation in ability to acquire resources, however, we were not able to test this hypothesis.

We expected the expression of early growth to be also less prevalent in males as compensational processes are suggested to be more likely in populations not limited by food (e.g. Albon et al. 1992; Gaillard et al. 1997a). However, the favourable feeding conditions on Vega did not seem to influence the relationship between juvenile and adult body mass of males, at least not to the age of 2 (Fig. 4). After observing a similar lack of compensation in a high performing population of fallow deer, Pélabon (1997) suggested that compensatory growth may not apply for highly polygynous species where sexual selection is likely to overrule the effect of good nutritional conditions on the ability to compensate. We believe that such an explanation may also hold in our case as large prime-aged male moose are also assumed to have a substantial reproductive advantage compared to smaller males (Bubenik 1998). To attain large size and ensure access to a higher number of females, young males may therefore benefit by growing as fast as possible during the subadult age-classes (Trivers 1972), independent of feeding condition and juvenile size, which may explain the absence of compensatory growth in males on Vega despite the excellent environmental conditions. However, given the low number of males above the age of 4 in our analyses, the results concerning the prime-aged males should be interpreted with caution.

Conclusions

The lack of substantial catch-up growth in moose agrees with a number of studies showing that the conditions during early development in long-lived species can have marked effects on the future performance of individuals (review in Lindström 1999; Metcalfe and Monaghan 2001; Gaillard et al. 2003). Because the calf body mass is likely to increase with maternal body mass, independent of age (Solberg et al. 2007), we also hypothesise that maternal and cohort effects may be transmitted between generations (review in Beckerman et al. 2002). Whether a similar pattern is present in moose populations more affected by density dependence and temporal fluctuations in environmental conditions remains to be seen. However, as environmental stochasticity may generate large variations in conditions for body growth until adulthood, we would expect weaker relationships between calf and adult body mass in more food-limited populations in which climatic perturbations have stronger effects (Herfindal et al. 2006). So far, results from studies of body growth in moose populations which are likely to be more influenced by food limitation (e.g. Cederlund et al. 1991; Sand 1996; Keech et al. 1999; Solberg et al. 2004) are ambiguous, and either based on weight differences over very short age-intervals (e.g. within the first year of age; Cederlund et al. 1991;

Keech et al. 1999: no compensatory growth) and/or based on comparison of means of cohorts rather than individuals (Solberg et al. 2004: some compensatory growth). To make us better understand the generality of our results, we therefore encourage more studies of individual body growth in low performance moose populations.

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