

Ageing and reproductive effort in male moose under variable levels of intrasexual competition

ATLE MYSTERUD*, ERLING J. SOLBERG† and NIGEL G. YOCCOZ‡§

*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, N-0316 Oslo, Norway; †Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway; ‡Institute of Biology, University of Tromsø, N-9037 Tromsø, Norway; and §Department of Arctic Ecology, Norwegian Institute for Nature Research, Polar Environmental Centre, N-9296 Tromsø, Norway

Summary

1. Capital breeding is a resource use tactic common among polygynous mammals, such as many ungulates. Even though large, prime-aged males stop eating during the rutting season, younger individuals often do not and may adopt alternative mating tactics that are less strenuous. The pattern of reproductive effort is therefore probably very variable among age classes, but has rarely been quantified in male mammals.
2. Based on data of body weight of 9949 male moose (*Alces alces* L.) aged up to 21 years from seven populations in Norway, we tested hypotheses regarding the pattern of reproductive effort (weight loss during rut) in this capital breeder, and how this may be affected by factors such as age, population sex ratio and density.
3. Reproductive effort increased with age, even after prime-age was reached around the age of 6 years. This provides the first evidence consistent with the terminal investment hypothesis in male mammals. For the very oldest males (> 12 years) data were limited, but the tendency was that effort stabilized or even decreased slightly. Effort did not depend on the population sex ratio or density for adult males.
4. Yearling males also lost some weight during the rutting season, but this was not related to population sex ratio. Decreasing trends in yearling body weight as seen in many strongly harvested moose populations, therefore are due probably to other causes than earlier onset of rutting. Further, effort in yearlings decreased with increasing density.
5. Despite the lack of a correlation between effort and population sex ratio, a significantly faster ageing after prime-age was observed with an increasingly female-biased population sex ratio. This is consistent with the hypothesis that strongly skewed sex ratios may affect the ageing process.
6. Most ungulate populations in Europe and North America are heavily harvested or otherwise managed extensively, harvest being typically male-biased to varying degrees. The resulting skews in sex ratio provide manipulations that give unique opportunities to study life-history variation, in particular for large mammals that are otherwise difficult to manipulate. These opportunities are currently not fully utilized.

Key-words: *Alces alces*, cost of reproduction, harvesting, life history, mating system, rutting, senescence.

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Introduction

Long-lived iteroparous animals face a challenge when deciding whether to allocate limited resources into

Correspondence: Atle Mysterud, Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, N-0316 Oslo, Norway. Tel: +47 22 85 40 45; Fax: +47 22 85 47 26; E-mail: atle.mysterud@bio.uio.no

current reproduction or rather saving it for survival and future fecundity (Stearns 1992). This trade-off is one of the cornerstones of life-history theory, and the optimal solution to this trade-off depends on factors such as sex and age of the individual. Resource use tactics for reproduction is often categorized along the capital-income breeding continuum (Stearns 1992; Jönsson 1997). Capital breeders rely heavily on accumulated body reserves to satisfy the energy needs of reproduction and

survival, while income breeders rely on food ingested during reproduction (Stearns 1992; Jönsson 1997). Species are often treated as having an obligate resource use strategy for reproduction (e.g. Andersen *et al.* 2000) but, for example, the aspic viper (*Vipera aspis* L.) may change from capital to income breeding under adverse environmental conditions (Lourdais *et al.* 2002). Variation in how much a capital breeder invests in current reproduction can also vary considerably depending on condition (Bonnet *et al.* 2002).

Males and females differ typically in the factors limiting reproductive success, particularly for highly sexually dimorphic birds and mammals (Darwin 1871; Andersson 1994). In strongly polygynous species, such as many ungulates, males fight fiercely with each other in order to gain access to mates during short rutting seasons (Clutton-Brock, Guinness & Albon 1982; Geist 1986; Gosling, Petrie & Rainy 1987; Festa-Bianchet *et al.* 1990; Komers, Messier & Gates 1994a), while females are limited mainly by raising young successfully (Clutton-Brock *et al.* 1982; Davies 1991). Most ungulates are considered as capital breeders. While females rely at least partly on ingested food during reproduction, and hence adopting a mix of capital and income breeding, many males adopt a pure capital breeding strategy during the rather brief rutting season. Age and size also affect the chosen reproductive strategy. Indeed, large, prime-aged moose (*Alces alces* L.) males stop eating during the rut, in contrast to smaller and younger individuals (Miquelle 1990). Prime-aged males often are able to monopolize harems (e.g. Clutton-Brock *et al.* 1982) or the best lekking places (e.g. Clutton-Brock, Deutsch & Nefdt 1993), and thereby access to most females. It may take 5 or 6 years or more to reach the body size necessary to be successful in intramale combat (Owen-Smith 1993). Many males are never able to achieve such a position, and variation in male reproductive success is larger than for females (Clutton-Brock *et al.* 1982). While giving priority to growth early in life, young males can nevertheless use alternative mating strategies that are less costly and gaining at least some copulations (e.g. Hogg 1984). This is known to lead to some paternity (Coltman *et al.* 2002; Preston *et al.* 2003). Population sex ratio may be predicted to have an effect on the level of male–male competition, but this has only been addressed to a limited extent (but see Komers *et al.* 1994a; Komers, Messier & Gates 1994b; Singer & Zeigenfuss 2002; Mysterud *et al.* 2003).

Phenotypical correlations provide a good assessment of the reproductive effort and cost of reproduction in capital breeders (Doughty & Shine 2001), and they are particularly useful for large herbivorous mammals in which experimental manipulation of reproductive effort is difficult (Festa-Bianchet, Gaillard & Jorgenson 1998). Based on data of body weight of 9949 male moose aged up to 21 years old from seven populations in Norway, we tested the following hypotheses regarding the pattern of reproductive effort (weight loss during the rut) in this capital breeder:

Hypothesis 1. *Terminal investment* (Williams 1966; Pianka & Parker 1975; Clutton-Brock 1984). The terminal investment hypothesis predicts increasing investment with age (after prime-age is reached) as residual reproductive value decreases. The pattern of reproductive effort over ages is used most commonly to test the ‘terminal investment’ hypothesis, although investment refers to parental effort relative to costs (Evans 1990). Increasing effort with age was observed in some studies in female ungulates (red deer *Cervus elaphus* L., Clutton-Brock 1984; moose: Ericsson *et al.* 2001), but not in others (reindeer *Rangifer tarandus* L., Weladji *et al.* 2002) and not for male red deer (Yoccoz *et al.* 2002) or bison (*Bison bison* L.) (Maher & Byers 1987).

Hypothesis 2. *Mating-strategy* (Yoccoz *et al.* 2002). Reproductive effort may be related more closely to the mating strategy adopted than to age *per se*. In male red deer, Yoccoz *et al.* (2002) found decreasing effort with age after prime-age, which may be explained by reduced ability of the oldest males to hold a harem. In contrast, male moose in forest areas usually adopt a strategy of sequential polygyny, defending one female at a time, and this strategy is stable as the males age (Bubenik 1998). For moose, then, the mating-strategy effort hypothesis predicts no change in effort with age, as no change in mating strategy is expected to occur.

Hypothesis 3. *Sex ratio and male–male competition* (Singer & Zeigenfuss 2002; Mysterud *et al.* 2003). Most large herbivore populations are heavily harvested, poached or otherwise managed, which often results in a sex ratio skewed towards females and with a young male age structure (Ginsberg & Milner-Gulland 1994; Langvatn & Loison 1999; Clutton-Brock *et al.* 2002; Mysterud, Coulson & Stenseth 2002; Milner-Gulland *et al.* 2003). Such conditions may decrease male–male competition for access to females. Most Norwegian moose populations are indeed heavily harvested and with a subsequent skewed sex ratio towards females and with a young male age structure (Solberg *et al.* 2002; Sæther, Solberg & Heim 2003). Reduced overall intrasexual competition can give variable predictions for yearling and older moose. (H_{3a}) Dominant, prime-aged males may experience less competition and hence lower effort with increasingly female-biased sex ratios. Yearling males are inferior in size and generally invest in further growth rather than in current reproductive effort. However, yearlings are sexually mature (e.g. Schwartz, Regelin & Franzmann 1982; Schwartz 1998; Coltman *et al.* 2002; Sæther *et al.* 2003) and (H_{3b}) effort may increase when male–male competition is low due to a skewed sex ratio (Komers *et al.* 1994a; Komers *et al.* 1994b; Mysterud *et al.* 2003). Further, as ageing may be linked to the cost of reproduction (Gustafsson & Pärt 1990), we may (H_{3c}) predict faster ageing with more female-biased population sex ratios, due to earlier breeding by young males.

Hypothesis 4. *Population density* (Yoccoz *et al.* 2002). Males may be expected to invest less with increasing density, as they are in poor condition at high density (Mysterud *et al.* 2001) and their chances of survival is

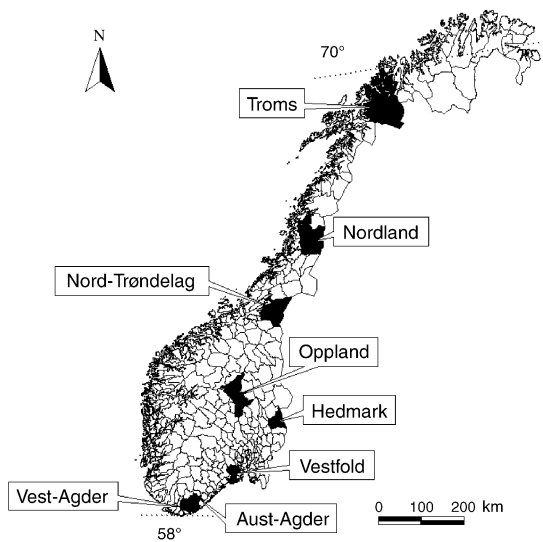


Fig. 1. A map of Norway showing the location for the eight counties with moose data included in this study. Aust-Agder and Vest-Agder constituted one region in the analyses.

correspondingly lower (Clutton-Brock, Rose & Guinness 1997). Therefore, they may not choose to deplete all their body reserves just prior to winter.

Materials and methods

MOOSE DATA

Data were collected during the annual autumn harvest 1991–2001 in Norway, and derive from 44 municipalities in the counties (*n* = no municipalities) Aust-Agder (*n* = 3), Vest-Agder (*n* = 5), Vestfold (*n* = 8), Oppland (*n* = 7), Hedmark (*n* = 3), Nord-Trøndelag (*n* = 6), Nordland (*n* = 3) and Troms (*n* = 9) (Fig. 1). Aust-Agder and Vest-Agder are adjacent to each other, and were therefore considered as one region. The data collection is part of the National Monitoring of cervids in Norway funded by the Directorate for Nature Management and performed by the Norwegian Institute for Nature Research (e.g. Solberg *et al.* 1997; Danielsen 2001). Data therefore cover most of the distribution range of moose

in Norway, and subsequently spanning a large variety of habitats.

Hunting is controlled through licenses issued by local wildlife boards in each municipality. The hunting period was from 25 September to 1 October and 10 October to 31 October in counties Aust-Agder, Nord-Trøndelag, Oppland and Troms, while the hunting period was from 5 October to 31 October in Hedmark, Vest-Agder and Vestfold counties. Hunters recorded sex, date, locality (municipality) and body weight. Body weight is carcass weight (approximately 50% of live weight, Wallin, Cederlund & Pehrson 1996), i.e. live weight minus head, skin, viscera, bleedable blood and metapodials (Langvatn 1977). The correlation between carcass weight and total weight is 0.994 in male moose (Wallin *et al.* 1996). Hunters also provided mandibles from all animals shot so that age could be determined from eruption patterns and tooth sectioning (Hamlin *et al.* 2000). Data consisted of 9949 individual male moose aged from 1 to 21 years (Table 1). As moose are shot through the whole rutting season, weight loss (i.e. reproductive effort) can be analysed as the effect of date of culling on body weight (Yoccoz *et al.* 2002). Total reproductive effort is then the difference between weight before and after the rutting season. We must therefore make the assumption that body mass adequately reflect condition.

As our data are transversal (i.e. comparing different animals shot at different times) and not longitudinal (i.e. following the same individuals over time), we have to make the critical assumption that there is no strong effect of natural or active hunter selection (between age classes or within the hunting season a given year). Hunting in Norway is mainly conducted using dogs (which smell the location of the moose) and a hunting team. Hunters may be selective when quota is small relative to population size (Solberg *et al.* 2000), and the very oldest age classes are somewhat more prone to being shot (because they are large or due possibly to factors such as reduced sight, vision or mobility; Ericsson & Wallin 2001). In our data, there was a weak negative relationship between age (strong correlate of size) and date of culling in five of seven regions (i.e. a higher proportion of older males shot first; Nordland: $r^2 = 0.0006$, $P = 0.303$; Oppland: $r^2 = 0.0017$, $P = 0.078$;

Table 1. Sample sizes for age classes of male moose by county in Norway

County/Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	21
Troms	716	152	74	34	16	8	3	1	2	1	3								
Nordland	927	455	273	129	59	23	13	3	5		1	2	1						
Nord-Trøndelag	1113	226	120	28	17	8	2	6		2	2	1				1			
Oppland	942	407	216	120	61	30	20	8	4	1	3	1	1	3	1		1		1
Hedmark	529	237	121	53	18	17	5	4		1	1	1							
Vestfold	782	169	126	53	30	13	14	3	4	4	2	1	2		1				
Aust Agder	507	200	102	60	28	18	9	6	2	3		2							1
Vest Agder	437	66	34	18	5	5	2	1	1	1	1			1				1	
Total	5953	1912	1066	495	234	122	68	32	18	13	13	8	4	4	2	1	2	1	1

Hedmark: $r^2 = 0.0028$, $P = 0.095$; Vestfold: $r^2 = 0.0007$, $P = 0.359$, but only one was significant (Troms: $r^2 = 0.0083$, $P = 0.004$). In two other regions, the relationship between age and date of culling was weakly positive (Nord-Trøndelag: $r^2 < 0.0001$, $P = 0.999$; Agder: $r^2 = 0.0022$, $P = 0.536$), with the same overall pattern of weight loss during rut and within the range of ageing in the other counties. Possibly, passive hunter selectivity may also influence on the distribution of sampled animals if the ability to avoid predators is condition-dependent. If moose in better condition are better able to avoid hunters and their dogs or, conversely, males in good condition may be more active in searching for females and therefore are encountered more often by hunters and their dogs, this may cause bias, in particular if animals in better or worse condition are also more or less likely to be shot at a specific time of the rut. Unfortunately, there is currently no information available to assess with confidence whether this is likely to occur, and this therefore awaits further study.

In Norway, all hunters (or hunting teams) report the number, age (calf or adult) and sex of moose seen each day (Solberg & Sæther 1999; Solberg *et al.* 1999). Based on this, we calculated both a density index (total number of moose observations per hunter day) and an index of population sex ratio (number of males : females reported) for each municipality and year. Such moose observations provide a reliable index of population density and structure at a large spatial scale such as municipality (Ericsson & Wallin 1999; Solberg & Sæther 1999; Solberg *et al.* 2002; see also Sylvén 2000).

As an index for the overall climatic conditions, we used the North Atlantic Oscillation (Hurrell's winter index; Hurrell *et al.* 2003; see review in Stenseth *et al.* 2002).

STATISTICAL ANALYSES

We used linear models (LM) for statistical analyses and polynomials to describe non-linear relationships, after some initial use of additive models (AM; Hastie & Tibshirani 1990) with smoothing splines to explore possible non-linear relationships graphically. A logarithmic transformation [$\ln(\text{weight})$] of body weight was used to get residuals with constant variance. By performing a logarithmic transformation of body weight, analysis of weight changes are seen on a relative scale so that differences between for example young and prime-aged males in the analysis are not due to differences in initial weight. We used one model including only yearlings and another model including males aged 2 years and older. This was performed as yearlings dominated the material (60%; Table 1), and as initial analyses showed that models were sensitive to what factors were included when a single global model was used because of complex interactions between age and other covariates when all age classes were included. This was not the case after splitting the material into these two categories. We also considered a separate model for

prime-aged individuals (6–12 years of age) to validate conclusions regarding Hypothesis 1 and Hypothesis 2 and to test Hypothesis 3c. As sample size was somewhat limited ($n = 274$, Table 1), we used bootstrapping (1000 replicates) to calculate standard errors (Efron & Tibshirani 1993).

To assess interactions between two continuous predictors (such as sex ratio and date), we restricted the analysis to a multiplicative term of the standardized (st) variables. The predictor variables were standardized (mean 0, variance 1) to facilitate the interpretation of the interaction and polynomial terms (as in e.g. Portier *et al.* 1998; Mysterud *et al.* 2001). The NAO index is already standardized (it is defined as a normalized pressure difference; Hurrell 1995). When variables are standardized, the coefficient for a variable included in an interaction term is the strength of this variable when the other variables in the interaction are average (because the interaction term is then zero). For a second-order polynomial, the linear term represents the slope at the average, and the quadratic term the curvature at the average. We included interactions for which there were specific predictions, such as for age*st(date) (to test for age-dependent reproductive effort; Hypotheses 1–2), st(date)*st(sex ratio) (to test for variation in effort with decreasing male–male competition; Hypothesis 3a–b) and st(date)*st(density) (to test for variation in effort with population density; Hypothesis 4). Variation in hunting tradition (e.g. lead dog vs. drive hunting) and, to some extent, habitat may provide differences in sightability of number of moose between regions (Solberg *et al.* 2002). Further, density dependence may also differ between neighbouring regions (e.g. Milner-Gulland, Coulson & Clutton-Brock 2000). We therefore, in addition, included interactions of several factors [e.g. year, NAO, st(density), st(sex ratio) and st(date)] with region. The index for population sex ratio can be compared easily between regions, as there are probably no biases, but for consistency we also tried an interaction term with region for this variable. Fitting a too-complex model would result in estimates with lower bias but lower precision, and it is most important to lower bias as much as possible (Cochran & Rubin 1973).

We used the Akaike information criterion (AIC; Burnham & Anderson 1998) for selecting an appropriate model for hypothesis testing. The model with the lowest AIC value is considered to be the most parsimonious model, i.e. the best compromise between explaining most of the variation and simultaneously using as few parameters as possible. We did not use automatic selection procedures as, for example, a third-order polynomial may give a much better fit than a first-order (i.e. linear) polynomial, but a second-order may not. We therefore systematically explored models with higher-order polynomials, as well as interaction terms. The detailed strategy when selecting models is given in tables (see below). All analyses were done in S-Plus vs. 6.0 (Venables & Ripley 1994).

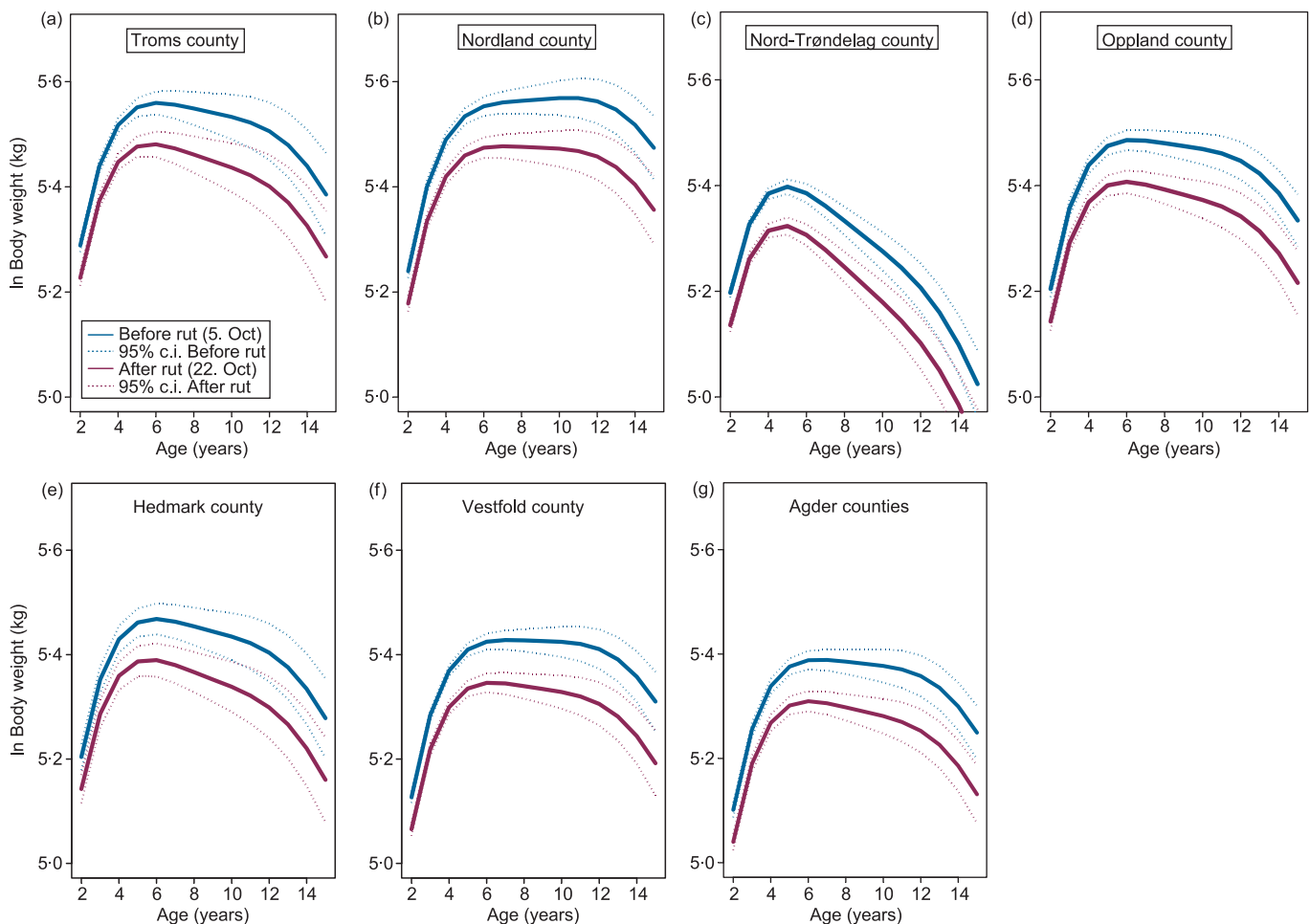


Fig. 2. The relationship between body weight and age in male moose in seven regions of Norway. For a given age category, the difference between the curve before (blue) and after (red) rut is an estimate of the weight loss and therefore of reproductive effort.

Results

The relationship between body weight and age was non-linear and best described by a fifth-order polynomial for age (Fig. 2; Table 2). The weight peaked at 6 years of age in five of seven regions, and then declined slightly until about 10–12 years of age, after which weight decreased more rapidly. The difference in estimates of body weight before and after rut (i.e. the parameter $st(date)$ estimating reproductive effort in males) was strongly dependent on male age [as estimated from the interaction $age*st(date)$; Tables 2 and 3]. Reproductive effort increased markedly with age (Fig. 2), also after prime-age (6 years of age) was reached, and we therefore retained Hypothesis 1, while this is not consistent with Hypothesis 2 (see Introduction). We had only 15 males older than 12 years of age so we cannot conclude with confidence, but the tendency was that effort stabilized or even decreased slightly for the oldest individuals (Fig. 2). The increase in effort with age was validated by the separate analysis with bootstrapping for prime-aged males between 6 and 12 years of age (Fig. 3, Tables 4 and 5).

The term $st(date)*st(sex\ ratio)$ entered the final model, suggesting that effort decreased the more sex

ratio was skewed towards females (Table 2). However, the term was not significant (Table 3), providing no solid support to Hypothesis 3a. This pattern did not change with age [as the term $age*st(date)*st(sex\ ratio)$ did not enter the most parsimonious model; Table 2] when comparing males aged 2 years or older. Population density did not affect rut-related weight loss [the term $st(density)*st(date)$ did not enter the model], thus Hypothesis 4 was not supported. In addition, male weights varied largely between regions, and the factors age, year (entered as a continuous variable) and density all interacted with region (Tables 2 and 3).

For different populations, weight both increased and decreased with age from 6 to 12 years of age (Fig. 2). In the model (using bootstrapping) considering individuals from 6 to 12 years of age, there was a significant correlation between ageing (i.e. the estimate for weight development from 6 to 12 years of age) and the population sex ratio (Tables 4 and 5). Ageing was faster the more female-biased the sex ratio (Fig. 3). Therefore, we found a pattern consistent with Hypothesis 3c.

Yearling males also lost some weight during the rutting season (Tables 6 and 7). There was no solid evidence that weight loss was related to (Hypothesis 3b) sex ratio,

Table 2. Results from model selection performed on $\ln(\text{weight})$ for male moose aged 2 years and older. x = term included in model. AIC = Akaike information criteria; ΔAIC = difference in AIC value between the AIC for the model given in that row and the most parsimonious model (lowest AIC). The most parsimonious model (bold type) explained 48.3% of the variation, and was used for parameter estimation (Table 3)

Age	(Age) ²	(Age) ³	(Age) ⁴	(Age) ⁵	(Age) ⁶	County	Year	NAO	st(density)	st(sex ratio)	st(date)	st(date) ²	st(date) ³	st(date) ⁴	st(date)*st(sex ratio)	st(date)*st(density)	Age*st(date)	Age*st(date) ²	Age*st(date) ³	(Age) ² *st(date)	Age*st(sex ratio)	(Age) ³ *st(sex ratio)	Age*st(density)	Age*st(date)*st(sex ratio)	Age*st(date)*st(density)	County*Age	County*(Age) ²	County*Year	County*NAO	County*st(density)	County*st(sex ratio)	County*st(date)	County*st(date)*st(sex ratio)	County*st(date)*st(density)	County*Age*st(date)*st(density)	AIC	ΔAIC	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4224.587	64.276
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4232.372	56.491
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4242.573	46.290
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4249.196	39.667
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4258.143	30.720
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4267.523	21.340
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4264.096	24.767
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4271.961	16.902
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4251.457	37.406
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4277.200	11.663
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4261.967	26.896
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4277.698	11.165
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4279.206	9.657
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4279.387	9.476
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4269.058	19.805
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4220.520	68.343
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4281.145	7.718
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4282.833	6.030
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4284.484	4.379
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4286.257	2.606
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4282.056	6.807
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4284.045	4.818
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4287.054	1.809
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4287.103	1.760
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4286.849	2.014
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4285.789	3.074
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4288.067	0.796
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4288.612	0.251
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4288.595	0.268
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4288.762	0.101
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4288.863	0.000
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4287.098	1.765
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4285.545	3.318
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4287.387	1.476
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-4288.307	0.556

as even though the interaction term $\text{st}(\text{date}) * \text{st}(\text{sex ratio})$ entered the final model (Table 6), it was not significant (Table 7). However, effort was related to (Hypothesis 4) density (i.e. interaction term $\text{st}(\text{date}) * \text{st}(\text{density})$) among yearlings, and effort decreased with increasing density. There was substantial variation in yearling weight between regions, and both the covariate year, the NAO, density, sex ratio and date interacted with region (Tables 6 and 7). Note that the effect of density therefore was both positive and negative in different regions. Common for those with a positive effect of density was a very low variance in density during the study period (Troms, Nord-Trøndelag and Oppland: within-region variation between 0.03 and 0.05 moose

seen per day), while those with negative density dependence had more variation in density (Hedmark, Vestfold and Agder; variation between 0.13 and 0.22 moose seen per day).

Discussion

Our study indicates that reproductive effort of a typical capital breeder, male moose, increased with age, even after prime-age was reached (Fig. 2). Further, effort seemed to decrease with density in yearlings. Effort in adult moose was not related to either population sex ratio or density. Despite this, ageing (weight development from 6 to 12 years of age) was faster the more

Table 3. Parameter estimates and test statistics for the analysis of $\ln(\text{weight})$ for male moose aged 2 years and older, based on the model with the lowest AIC value (AIC = -4288.863; Table 2). These estimates are the ones used for drawing Fig. 2. The main terms of interest is Age, $\text{st}(\text{date})$ (estimation of weight loss during rut), $\text{st}(\text{sex ratio})$ (estimation of male-male competition), $\text{Age}*\text{st}(\text{date})$ (estimation of age dependent weight loss during rut), $\text{st}(\text{date})*\text{st}(\text{sex ratio})$ (estimation of differences in weight loss during rut depending on level of male-male competition) and higher order terms for some of these factors

Parameter	l.s. estimate	SE	T	P
(Intercept)	6.9014	4.5845	1.505	0.132
Age	0.5026	0.0439	11.459	0.000
(Age) ²	-0.1032	0.0137	-7.542	0.000
(Age) ³	0.0101	0.0018	5.538	0.000
(Age) ⁴	-0.0005	0.0001	-4.472	0.000
(Age) ⁵	0.0000	0.0000	3.806	0.000
County Nordland vs. Troms	0.6950	5.3960	0.129	0.898
County Nord-Trøndelag vs. Troms	-9.0520	6.0861	-1.487	0.137
County Oppland vs. Troms	-3.6130	5.4505	-0.663	0.507
County Hedmark vs. Troms	-3.1709	6.9477	-0.456	0.648
County Vestfold vs. Troms	19.2205	6.2595	3.071	0.002
County Agder vs. Troms	10.2333	6.4505	1.586	0.113
Year (continuous)	-0.0011	0.0023	-0.497	0.620
$\text{st}(\text{density})$	0.0219	0.0133	1.652	0.099
$\text{st}(\text{sex ratio})$ (males per female)	0.0066	0.0039	1.685	0.092
$\text{st}(\text{date})$	-0.0367	0.0051	-7.224	0.000
$\text{st}(\text{sex ratio})*\text{st}(\text{date})$	-0.0038	0.0027	-1.443	0.149
$\text{Age}*\text{st}(\text{date})$	-0.0051	0.0018	-2.779	0.006
$\text{Age}*\text{st}(\text{date})^2$	-0.0010	0.0010	-1.007	0.314
$\text{Age}*\text{st}(\text{date})^3$	0.0019	0.0006	3.458	0.001
$\text{Age}*\text{County Nordland vs. Troms}$	0.0106	0.0064	1.663	0.096
$\text{Age}*\text{County Nord-Trøndelag vs. Troms}$	-0.0208	0.0070	-2.979	0.003
$\text{Age}*\text{County Oppland vs. Troms}$	0.0025	0.0060	0.414	0.679
$\text{Age}*\text{County Hedmark vs. Troms}$	-0.0018	0.0073	-0.239	0.811
$\text{Age}*\text{County Vestfold vs. Troms}$	0.0066	0.0067	0.992	0.321
$\text{Age}*\text{County Agder vs. Troms}$	0.0039	0.0065	0.605	0.545
$\text{County Nordland vs. Troms}*\text{year}$	-0.0004	0.0027	-0.142	0.887
$\text{County Nord-Trøndelag vs. Troms}*\text{year}$	0.0045	0.0031	1.479	0.139
$\text{County Oppland vs. Troms}*\text{year}$	0.0018	0.0027	0.646	0.518
$\text{County Hedmark vs. Troms}*\text{year}$	0.0015	0.0035	0.444	0.657
$\text{County Vestfold vs. Troms}*\text{year}$	-0.0097	0.0031	-3.097	0.002
$\text{County Agder vs. Troms}*\text{year}$	-0.0052	0.0032	-1.617	0.106
$\text{County Nordland vs. Troms}*\text{density}$	-0.0379	0.0233	-1.626	0.104
$\text{County Nord-Trøndelag vs. Troms}*\text{density}$	-0.0100	0.0162	-0.619	0.536
$\text{County Oppland vs. Troms}*\text{density}$	0.0203	0.0224	0.905	0.365
$\text{County Hedmark vs. Troms}*\text{density}$	-0.0635	0.0286	-2.219	0.027
$\text{County Vestfold vs. Troms}*\text{density}$	-0.0310	0.0146	-2.123	0.034
$\text{County Agder vs. Troms}*\text{density}$	-0.0339	0.0157	-2.167	0.030

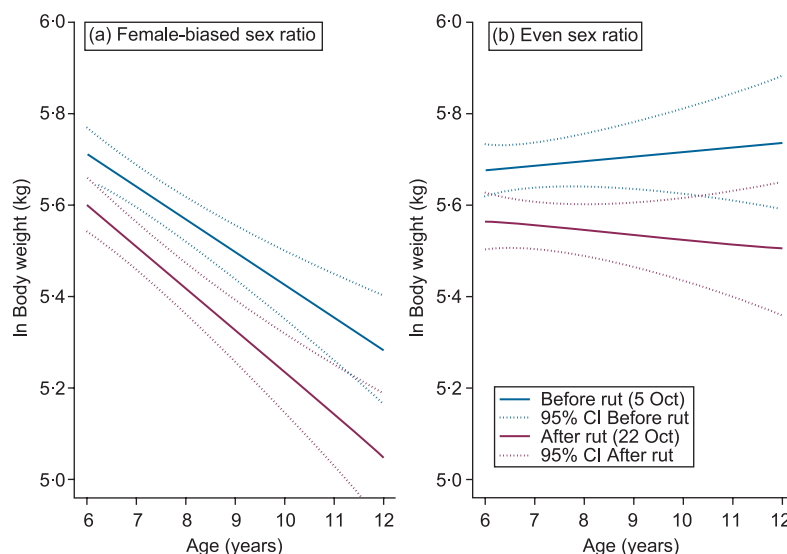


Fig. 3. The relationship between ageing (i.e. weight development from 6 to 12 years of age) and population sex ratio for male moose in Norway (printed for Troms county) before (blue) and after (red) rut.

Table 4. Results from model selection performed on $\ln(\text{weight})$ for male moose aged between 6 and 12 years of age. $x =$ term included in model. AIC = Akaike information criteria; ΔAIC = difference in AIC value between the AIC for the model given in that row and the most parsimonious model (lowest AIC). The most parsimonious model (bold type) was used for parameter estimation (Table 5)

Age	(Age) ²	(Age) ³	(Age) ⁴	(Age) ⁵	County	Year	NAO	st(density)	st(sex ratio)	st(date)	st(date) ²	st(date) ³	st(date)*st(sex ratio)	st(date)*st(density)	Age*st(date)	Age*st(date) ²	Age*st(date) ³	(Age) ² *st(date)	Age*st(sex ratio)	(Age) ² *st(sex ratio)	Age*st(density)	Age*st(date)*st(sex ratio)	Age*st(date)*st(density)	County*Age	County*(Age) ²	County*Year	County*.NAO	County*st(density)	County*st(sex ratio)	County*st(date)	County*st(date)*st(sex ratio)	County*st(date)*st(density)	County*Age*st(date)*st(density)	AIC	ΔAIC		
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-156.062	62.552	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-161.246	57.368	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-168.454	50.160	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-172.793	45.821	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-175.792	42.822	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-174.896	43.718	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-181.661	36.953	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-184.593	34.021	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-192.638	25.976	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-190.456	28.158
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-194.244	24.370
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-193.037	25.577
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-194.993	23.621
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-194.037	24.577
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-193.129	25.485
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-196.943	21.671
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-197.126	21.488
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-197.942	20.672
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-199.174	19.440
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-190.265	28.349
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-199.727	18.887
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-200.112	18.502
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-201.574	17.040
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-201.574	17.040
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-207.696	10.918
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-210.002	8.612
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-202.702	15.912
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-210.550	8.064
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-212.000	6.614
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-207.971	10.643
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-213.520	5.094
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-202.986	15.628
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-204.719	13.895
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-214.926	3.688
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-216.253	2.361
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-218.253	0.361
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-218.614	0
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-216.623	1.991
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-214.634	3.980

female-biased the sex ratio. This holds under the critical assumption of no strong effect of natural or hunter selection (between age classes or within the hunting season a given year), as the current analyses are based on transversal (i.e. comparing different animals shot at different times) and not longitudinal (i.e. following the same individuals over time) data. Specifically, we assume that animals in better or worse condition are *not* more or less likely to be shot at a specific time of the rut (see Methods).

Our study is in line with a number of previous studies of male ungulates reporting that reproductive effort increases with age from yearlings to the prime-aged stage (bison: Maher & Byers 1987; reindeer: Kojola 1991; Mysterud *et al.* 2003; red deer: Yoccoz *et al.* 2002; review in Mysterud, Langvatn & Stenseth 2004). However, our study is the first evidence presented that is consistent with the terminal investment hypothesis (Hypothesis 1), which predicts an increase in effort after prime-age is reached (as residual reproductive

Table 5. Parameter estimates (using bootstrapping) for the analysis of $\ln(\text{weight})$ for male moose aged between 6 and 12 years of age, based on the model with the lowest AIC value (AIC = -218.614; Table 4). These estimates are the ones used for drawing Fig. 3. The main terms of interest is Age, $\text{st}(\text{date})$ (estimation of weight loss during rut), $\text{st}(\text{sex ratio})$ (estimation of male–male competition), $\text{Age}*\text{st}(\text{date})$ (estimation of age dependent weight loss during rut), $\text{Age}*\text{st}(\text{sex ratio})$ (estimation of ageing depending on level of male–male competition) and higher order terms for some of these factors

	I.s. estimate	Bootstrap estimate	Bootstrap SE	Lower 95% CI	Upper 95% CI
(Intercept)	5.8807	5.8833	0.1499	5.5835	6.1830
Age	-0.0333	-0.0334	0.0193	-0.0721	0.0053
County Nordland vs. Troms	-0.4275	-0.4267	0.1844	-0.7956	-0.0579
County Nord-Trøndelag vs. Troms	-0.0555	-0.0559	0.2256	-0.5071	0.3954
County Oppland vs. Troms	-0.5994	-0.6014	0.1755	-0.9525	-0.2504
County Hedmark vs. Troms	-0.0894	-0.0916	0.2149	-0.5213	0.3381
County Vestfold vs. Troms	-0.4924	-0.4915	0.1874	-0.8663	-0.1167
County Agder vs. Troms	-0.4185	-0.4227	0.1731	-0.7689	-0.0765
$\text{st}(\text{sex ratio})$	0.1760	0.1780	0.0704	0.0373	0.3188
$\text{st}(\text{date})$	0.0060	0.0065	0.0479	-0.0893	0.1024
$\text{Age}*\text{st}(\text{date})$	-0.0134	-0.0133	0.0068	-0.0270	0.0003
$\text{Age}*\text{st}(\text{date})^2$	-0.0048	-0.0047	0.0017	-0.0081	-0.0013
$\text{Age}*\text{st}(\text{date})^3$	0.0039	0.0038	0.0011	0.0017	0.0059
$\text{Age}*\text{st}(\text{sex ratio})$	-0.0273	-0.0276	0.0104	-0.0483	-0.0068
$\text{Age}*\text{County Nordland vs. Troms}$	0.0504	0.0498	0.0245	0.0009	0.0987
$\text{Age}*\text{County Nord-Trøndelag vs. Troms}$	-0.0362	-0.0363	0.0291	-0.0945	0.0219
$\text{Age}*\text{County Oppland vs. Troms}$	0.0614	0.0615	0.0230	0.0155	0.1074
$\text{Age}*\text{County Hedmark vs. Troms}$	-0.0075	-0.0075	0.0285	-0.0646	0.0495
$\text{Age}*\text{County Vestfold vs. Troms}$	0.0418	0.0415	0.0241	-0.0067	0.0898
$\text{Age}*\text{County Agder vs. Troms}$	0.0275	0.0279	0.0225	-0.0172	0.0729

Table 6. Results from model selection performed on $\ln(\text{weight})$ for yearling male moose. $x =$ term included in model. AIC = Akaike Information Criteria; ΔAIC = difference in AIC value between the AIC for the model given in that row and the most parsimonious model (lowest AIC). The most parsimonious model (bolded) explained 21.5% of the variation, and was used for parameter estimation (Table 7)

County	Year	NAO	$\text{st}(\text{density})$	$\text{st}(\text{sex ratio})$	$\text{st}(\text{date})$	$\text{st}(\text{date})^2$	$\text{st}(\text{date})^3$	$\text{st}(\text{date})^4$	$\text{st}(\text{date})*\text{st}(\text{sex ratio})$	$\text{st}(\text{date})*\text{st}(\text{density})$	County*Year	County*NAO	County* $\text{st}(\text{density})$	County* $\text{st}(\text{sex ratio})$	County* $\text{st}(\text{date})$	County* $\text{st}(\text{date})*\text{st}(\text{sex ratio})$	County* $\text{st}(\text{date})*\text{st}(\text{density})$	AIC	ΔAIC
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7006.389	19.624
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7015.729	10.284
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7024.174	1.839
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7021.784	4.229
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-6978.385	47.628
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-6969.605	56.408
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7015.258	10.755
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-6980.315	45.698
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7022.457	3.556
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7023.688	2.325
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7022.480	3.533
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7026.013	0
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-7025.570	0.443

value increases, see Introduction) in male ungulates or other mammals, although earlier reported for females including the moose (Ericsson *et al.* 2001). In contrast to our study, decreased effort after prime-age was reported for male bison (Maher & Byers 1987) and red deer (Yoccoz *et al.* 2002). This decrease in effort for the oldest age-classes in red deer was suggested related to

the change in mating strategy from prime-age to the senescent stage (Yoccoz *et al.* 2002), as the very oldest males are not able to defend a harem (Clutton-Brock *et al.* 1982). Also male bison may adopt different mating strategies as they age (Komers, Messier & Gates 1992). Our case, where we expect no change in the mating strategy with age, provides therefore an interesting

Table 7. Parameter estimates and test statistics for the analysis of $\ln(\text{weight})$ for yearling male moose, based on the model with the lowest AIC value (AIC = -7026.013; Table 6). The main terms of interest is $\text{st}(\text{date})$ (estimation of weight loss during rut), $\text{st}(\text{sex ratio})$ (estimation of male-male competition), $\text{st}(\text{date}) * \text{st}(\text{sex ratio})$ (estimation of differences in weight loss during rut depending on level of male-male competition) and higher order terms for some of these factors

Parameter	l.s. estimate	SE	T	P
Intercept	16.0350	3.6215	4.428	0.000
County Nordland vs. Troms	-11.8981	4.8451	-2.456	0.014
County Nord-Trøndelag vs. Troms	-9.4500	4.5587	-2.073	0.038
County Oppland vs. Troms	-4.2137	4.7620	-0.885	0.376
County Hedmark vs. Troms	-8.9984	6.4426	-1.397	0.163
County Vestfold vs. Troms	16.1062	4.8987	3.288	0.001
County Agder vs. Troms	-13.1821	5.0692	-2.600	0.009
Year (continuous)	-0.0055	0.0018	-3.046	0.002
NAO	0.0065	0.0021	3.036	0.002
$\text{st}(\text{density})$	0.0146	0.0071	2.044	0.041
$\text{st}(\text{sex ratio})$ (males per female)	-0.0009	0.0048	-0.179	0.858
$\text{st}(\text{date})$	-0.0142	0.0047	-3.007	0.003
$\text{st}(\text{date})^2$	-0.0032	0.0020	-1.557	0.120
$\text{st}(\text{date}) * \text{st}(\text{sex ratio})$	-0.0039	0.0024	-1.605	0.109
$\text{st}(\text{date}) * \text{st}(\text{density})$	0.0053	0.0027	1.934	0.053
County Nordland vs. Troms*year	0.0059	0.0024	2.449	0.014
County Nord-Trøndelag vs. Troms*year	0.0047	0.0023	2.054	0.040
County Oppland vs. Troms*year	0.0020	0.0024	0.856	0.392
County Hedmark vs. Troms*year	0.0045	0.0032	1.378	0.168
County Vestfold vs. Troms*year	-0.0081	0.0025	-3.309	0.001
County Agder vs. Troms*year	0.0065	0.0025	2.576	0.010
County Nordland vs. Troms*NAO	-0.0046	0.0031	-1.475	0.140
County Nord-Trøndelag vs. Troms*NAO	-0.0103	0.0029	-3.540	0.000
County Oppland vs. Troms*NAO	-0.0019	0.0032	-0.587	0.558
County Hedmark vs. Troms*NAO	-0.0032	0.0040	-0.793	0.428
County Vestfold vs. Troms*NAO	-0.0097	0.0030	-3.187	0.001
County Agder vs. Troms*NAO	-0.0095	0.0038	-2.520	0.012
County Nordland vs. Troms* $\text{st}(\text{density})$	-0.0210	0.0258	-0.811	0.418
County Nord-Trøndelag vs. Troms* $\text{st}(\text{density})$	0.0076	0.0086	0.880	0.379
County Oppland vs. Troms* $\text{st}(\text{density})$	0.0339	0.0156	2.168	0.030
County Hedmark vs. Troms* $\text{st}(\text{density})$	-0.1273	0.0426	-2.990	0.003
County Vestfold vs. Troms* $\text{st}(\text{density})$	-0.0381	0.0091	-4.173	0.000
County Agder vs. Troms* $\text{st}(\text{density})$	-0.0324	0.0096	-3.356	0.001
County Nordland vs. Troms* $\text{st}(\text{sex ratio})$	0.0039	0.0122	0.321	0.748
County Nord-Trøndelag vs. Troms* $\text{st}(\text{sex ratio})$	-0.0268	0.0100	-2.684	0.007
County Oppland vs. Troms* $\text{st}(\text{sex ratio})$	0.0453	0.0090	5.039	0.000
County Hedmark vs. Troms* $\text{st}(\text{sex ratio})$	0.0281	0.0114	2.461	0.014
County Vestfold vs. Troms* $\text{st}(\text{sex ratio})$	-0.0133	0.0086	-1.550	0.121
County Agder vs. Troms* $\text{st}(\text{sex ratio})$	0.0195	0.0095	2.047	0.041
County Nordland vs. Troms* $\text{st}(\text{date})$	0.0002	0.0062	0.032	0.974
County Nord-Trøndelag vs. Troms* $\text{st}(\text{date})$	-0.0092	0.0065	-1.425	0.154
County Oppland vs. Troms* $\text{st}(\text{date})$	0.0153	0.0068	2.257	0.024
County Hedmark vs. Troms* $\text{st}(\text{date})$	0.0111	0.0103	1.078	0.281
County Vestfold vs. Troms* $\text{st}(\text{date})$	-0.0099	0.0091	-1.089	0.276
County Agder vs. Troms* $\text{st}(\text{date})$	-0.0014	0.0087	-0.158	0.874

case, showing that under such conditions the terminal investment hypothesis may apply. The cost of investment in rutting may therefore be much more pronounced in red deer than in moose. Interestingly, ageing was also much faster in red deer (Yoccoz *et al.* 2002) compared to moose (Fig. 2). In this study, a 6-year-old male moose (from Troms county) weighing 262 kg before the rut would lose 23 kg or 9% of the body weight in about 3 weeks' time, while a 12-year-old weighing 248 kg would lose 27 kg or 11% (Fig. 2). This is slightly lower than previous recorded weight losses of 12–19% of male moose during the rut in Alaska (Schwartz 1998), and is much less than for prime-aged red deer that can

lose up to 40% (Bobek, Perzanowski & Weiner 1990). This interspecific variation fits the expectation of the overall level of sexual selection based on the degree of sexual body-size dimorphism (male : female weight), which is 1.3 for moose and 1.5 for red deer (Loison *et al.* 1999b). For the very oldest males (> 12 years), effort stabilized or even tended to decrease slightly (Fig. 2). In most other studies in the literature, data from old, senescent individuals is usually either absent or not separated from prime-aged individuals.

Yearling males are a particularly interesting case, as they can adopt a number of alternative mating tactics (Hogg 1984) and may be more or less involved in

rutting depending on the level of intrasexual competition. Yearling reindeer (Mysterud *et al.* 2003) and bison (Komers *et al.* 1994a) reduced reproductive effort when many prime-aged males were present. It has been suggested previously that the temporal trends of reduced body weights of yearling male moose was due to earlier rutting that hampered body growth as the sex ratio became more skewed (Solberg & Sæther 1994). However, yearling moose were not varying their effort strongly depending on sex ratio (Table 7). Rather, the temporal trend of smaller yearlings with an increasingly female-biased sex ratio (Solberg & Sæther 1994) may be due more probably to density dependence and possible also delayed calving (Sæther *et al.* 2003; review in Mysterud *et al.* 2002), as yearling weight in autumn was correlated with autumn calf weights (Sæther *et al.* 2003). Effort in yearlings decreased with increasing density, as was found earlier in red deer, and was suggested to be related to poorer condition at high density (Yoccoz *et al.* 2002).

Much effort has been devoted recently to demonstrate empirically the presence of senescence in performance of a number of ungulate species (e.g. Loison *et al.* 1999a; Ericsson *et al.* 2001; Weladji *et al.* 2002), also in males (Mysterud *et al.* 2001; McElligott, Altwegg & Hayden 2002; Yoccoz *et al.* 2002). We found a decrease in body weight after 6 years in five of seven regions, and rate of senescence increased after 12 years of age was reached (Fig. 2). High-quality individuals may be expected to have a longer life span (Gaillard *et al.* 2000), and reproductive performance can therefore increase when comparing average performance of age classes (Laaksonen, Korpimäki & Hakkarainen 2002). Our estimates on senescence are therefore probably somewhat conservative. Both evolutionary-based hypotheses of senescence, the mutation–accumulation hypothesis (Medawar 1946; Edney & Gill 1968) and the antagonistic pleiotropy hypothesis (Medawar 1946; Williams 1957; Hamilton 1966; Rose 1991) as well as the disposable soma theory (review in Kirkwood & Austad 2000), predict a trade-off between current reproductive effort and senescence. Early onset of rutting activities in males due to a female-biased sex ratio caused by harvesting may therefore also affect the ageing process. Between populations, weight both increased and decreased from 6 to 12 years of age (Fig. 2), and ageing (weight development from 6 to 12 years of age) was indeed related significantly to population sex ratio (Hypothesis 3c; Fig. 3). It remains to be explained why a skew in population sex ratio towards females have no or marginal effect on current effort, while still affecting the ageing process. Clearly, following the same individual in the course of rut would provide better insight, but it is difficult to obtain such data.

Most ungulate populations in Europe and North America are heavily harvested or otherwise managed extensively. The direct effects of removing individuals on population dynamics are obvious (Langvatn & Loison 1999). As such harvesting is typically male-biased

to varying degrees (Langvatn & Loison 1999; Clutton-Brock *et al.* 2002), there are also indirect effects on calving rates and dates due to changes in the behavioural ecology of rutting (e.g. Laurian *et al.* 2000; Holand *et al.* 2003; Sæther *et al.* 2003; review in Mysterud *et al.* 2002). Recently, the sex ratio in a population of Saiga antelope (*Saiga tatarica* L.) in Kalmykia, Russia was reported to be below 1% of adult males (Milner-Gulland *et al.* 2003), following severe poaching of males (due to horns being used in Chinese medicine). This even led to a severe drop in fecundity, and females were seemingly fighting for access to males (Milner-Gulland *et al.* 2003). Also, for Norwegian moose there was a lower proportion of primiparous moose breeding when sex ratio became extremely female-biased (Solberg *et al.* 2002). Although the applied value of such information is obvious, such manipulations have only been used to a small extent to gain insight into the life history of males, as in the current paper. These opportunities are especially valuable as large herbivores are usually difficult to manipulate by researchers alone. The subsequent evolutionary consequences may not be trivial to predict, as opposing selection pressures, due to pleiotropic effects, may be involved (Kruuk *et al.* 2002). To exploit such possibilities fully, it is also important to recognize the possible biases due to the hunting (sampling) process. In order to gain further insight in the future we aim at modelling such processes explicitly to assess potential bias, based on procedures to model observational studies and missing data (Little & Rubin 1987; Rosenbaum 1995).

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