

The timing of male reproductive effort relative to female ovulation in a capital breeder

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Summary

1. In large herbivores, the timing of breeding is important for females to hit peak plant protein levels. For males, the timing of reproductive effort is important to maximize the number of females they can mate during autumn rut in competition with other males. The latter depends on when most females are ovulating, but also on how other males with a different competitive ability are timing use of their capital (fat); it may pay younger males to invest more heavily later when prime aged males are exhausted.

2. Based on estimates of body mass loss, we quantify how much timing (start, peak and end dates) of male reproductive effort during rutting varies depending on male age, density and climate as well as timing of female ovulation.

3. Ovulation in adult females was delayed by 5 days from low to high density, and ovulation was also more synchronous at high density. The starting date of decline in male body mass was only later in yearlings than among other age groups. However, at low density, peak and end dates of rut became increasingly earlier and close to peak female ovulation with increasing age up to 7 years of age. Prime-aged males matched peak effort closely with peak rate of prime-aged female ovulation, while younger males were delayed. This is consistent with the view that younger males have a better chance when the prime-aged males are becoming exhausted.

4. Apart from yearlings, male age groups were synchronized in both the starting, peak and end dates of mass decline at high density. Thus, this partly follows change in female ovulation patterns, but also suggests that competition among males decreased with increasing density due probably to lower intensity of sexual selection. The lowered sexual selection may be due not only to more synchronous female ovulation, but also increasingly female-biased sex ratios and a younger male age structure with increasing density.

5. The onset of rutting is somewhat independent of male age (apart from the youngest males), but the peak and end of rutting effort is dependent strongly upon age, density and peak female ovulation. Male rutting phenology is thus best interpreted as a compromise between hitting peak female ovulation and intensity of sexual selection.

Key words: body mass, cost of reproduction, density, ovulation, red deer

Introduction

Phenology is the study of seasonal plant and animal activity driven by environmental factors. In seasonal environments, many ecological processes occurring in animal populations are synchronized with plant phenology, such as migration, reproduction and breeding. In large herbivores, the timing of

birth in spring is essential for females in order to hit peak plant protein levels to support the costs of reproduction (e.g. Festa-Bianchet 1988; Loe *et al.* 2005). The factors affecting timing of male reproduction in ungulates have received much less attention, but probably differ substantially from that of females. While female reproductive success is limited mainly by gestation and lactation costs, male reproductive success, especially of dimorphic species, is limited by access to mates (Clutton-Brock, Albon & Guinness 1988). For obvious

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reasons, in order to reproduce successfully a male needs to be available for mating in the short time window in which the female is ready to conceive (about 24 h, Clutton-Brock, Guinness & Albon 1982). However, to gain access to females is not an easy task, and may involve fighting with other males for access (Geist 1974; Clutton-Brock *et al.* 1979), patrolling territories (Alvarez 1993), roaring contests (McComb 1987) and tending females (Hogg 1984; Hogg & Forbes 1997; Pelletier, Hogg & Festa-Bianchet 2006). The more time that is devoted to rutting activities, the less time is available for foraging (Willisch & Ingold 2007), and prime-aged males may stop eating completely (Maher & Byers 1987; Miquelle 1990). Most polygynous herbivores are capital breeders (Jönsson 1997; Festa-Bianchet, Gaillard & Jorgenson 1998). As a consequence of these energy-consuming activities and reduced time spent feeding, males lose condition as rut precedes (e.g. Kojola 1991; Yoccoz *et al.* 2002; Forsyth *et al.* 2005; Mysterud, Solberg & Yoccoz 2005). Only one study has addressed how males of different age classes are timing their effort within a rutting season relative to female oestrus or ovulation pattern, and they found that highly competitive males match female oestrus more effectively than other males (Preston, Stevenson & Wilson 2003).

In this study of a capital breeding and highly polygynous ungulate, the red deer (*Cervus elaphus*), we present a joint analysis of timing of male reproductive effort assessed from body mass loss relative to female rutting phenology (ovulation). We extend a previous analysis of mass loss in males (Yoccoz *et al.* 2002) and ovulation in females (Langvatn *et al.* 2004) with an explicit quantification of the timing of mass loss and ovulation rates using threshold models to assess the phenology of rutting effort; when they start to rut, when they peak in effort and when they end rutting relative to female ovulation pattern. We test the following not mutually exclusive hypotheses.

Hypothesis 1: males track female phenology

Even though males usually initiate rutting activities well before females, it is somewhat intuitive to predict that males will use most energy when females are receptive to mating. Thus, a delay in female oestrus and ovulation will delay peak effort of males. For instance, in Soay sheep (*Ovis aries*), competitive males time their mate-guarding to occur close to the optimal insemination period (Preston *et al.* 2003). As female ovulation is delayed with increasing density, but seems not to be linked to variation in the North Atlantic Oscillation (NAO) (Langvatn *et al.* 2004), we expect a later phenology at high than at low density, but no effect of the NAO. Consequently, as female oestrus and ovulation will be delayed, we predict a delayed peak effort of males at high density but no NAO effect on male rutting pattern.

Hypothesis 2: age determines phenology

Young males are less likely to compete successfully in male–male combat, and paternity in polygynous species is highly

skewed towards prime-aged males (e.g. Pemberton *et al.* 1992; Coltman *et al.* 2002). Younger males have a higher chance to sire later in rut, when prime-aged males are exhausted, or in species with sperm competition, due to depletion of sperm in prime-aged males (Preston *et al.* 2001). Indeed, several studies indicate that younger males start rutting at a later date than prime-aged males (review in Mysterud, Langvatn & Stenseth 2004), but no study has quantified how this varies with density or climate. If competition among males is high (higher sexual selection intensity), we would expect age classes (that differ in competitive ability) to be less synchronous, as younger males would have less chances for mating during peak rut. This yields the prediction that males should be more synchronous at high density, as sexual selection forces are likely to be weaker (Clutton-Brock & Parker 1992; but see Stutchbury & Morton 1995 for an alternative argument in songbirds); because female ovulation is more synchronous at high density (Langvatn *et al.* 2004); and because population sex ratio is probably more female-biased and male age structure younger with increasing density in these populations (due to heavy male harvest; Milner *et al.* 2006).

Materials and methods

STUDY AREA

The study area comprises large parts of the Norwegian South West coast, covering six Norwegian counties: Rogaland (number of municipalities; $n = 6$) and Hordaland ($n = 21$; termed population 'P1'), Sogn og Fjordane ($n = 23$; termed population 'P2'), Møre og Romsdal ($n = 25$) and Sør Trøndelag ($n = 13$; termed population 'P3') and Nord Trøndelag ($n = 2$; termed population 'P4'). The island Hitra in Sør Trøndelag is termed population 'P5'. The vegetation on the West coast of Norway is mainly in the boreo nemoral zone (Abrahamsen *et al.* 1977). A detailed description of the (forested) habitat (Mysterud *et al.* 2002) and (steep and hilly) topography (Mysterud *et al.* 2001a,b) is given elsewhere.

RED DEER DATA

Body mass, size and age

Male and female red deer were sampled during the annual autumn harvest 1965–2003 (e.g. Mysterud *et al.* 2001b; Langvatn *et al.* 2004). Compared to the data analysed by Yoccoz *et al.* (2002) on male reproductive effort, we added data from 2000 to 2003 (7821 males 1 year and older with exact body mass; thus totalling 22 414 males, Table 1). The hunting period lasts from 10 September to 15 November, covering the prerut and rut period. Assuming non-selective harvesting (see below), the effect of date of culling on (age specific) body mass will estimate (age-specific) mass loss over time (termed rutting or male effort). Until 2000 hunting was not permitted during 1 October to 10 October, which made it difficult to establish the exact start of rutting for all male age classes.

Hunting is controlled through licences issued by local wildlife boards in each municipality. In cooperation with local wildlife boards, hunters provided mandibles from all animals shot, together with records of sex, date, locality (municipality) and body mass. Body mass is dressed mass (i.e. live mass minus head, skin, viscera,

Table 1. Overview of sample sizes per age for high- and low-density periods for red deer along the West coast of Norway

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	≥ 20	Sum
Males																					
High density	4589	3249	1980	816	424	247	129	91	54	34	24	10	14	3	5	1	1	1	2		11 674
Low density	4399	3190	1566	637	384	240	123	89	44	25	22	7	3	4	3	1	0	3	0		10 740
Total	8988	6439	3546	1453	808	487	252	180	98	59	46	17	17	7	8	2	1	4	2		22 414
Females																					
High density	1321	1000	823	378	259	236	193	122	110	85	88	56	44	38	25	20	22	9	11	29	4 869
Low density	1196	1162	885	446	314	243	198	149	126	79	77	68	53	49	35	24	18	15	13	40	5 190
Total	2517	2162	1708	824	573	479	391	271	236	164	165	124	97	87	60	44	40	24	24	69	10 059

bleedable blood and metapodials). Dressed mass in hinds is about 58% of live mass (Langvatn 1977), and highly correlated ($r = 0.994$, $n = 127$) with total mass in Cervids (Wallin, Cederlund & Pehrson 1996). Age determination in calves and yearlings was based on tooth eruption patterns (Loe *et al.* 2004), whereas older animals were aged using annuli in the cementum of the first incisor (Hamlin *et al.* 2000).

Ovulation

As necessary background information of timing of female breeding, we also use data on ovulation that have been analysed in detail (Langvatn *et al.* 2004). Data ($n = 10\,073$) derive from the same source as the body mass data. Reproductive history of individual females can be estimated post mortem based on inspection of ovaries (Harrison & Weir 1977; Langvatn 1992). Ovulation can be assessed based on recording of a primary corpus luteum. As females are also harvested at different stages of the reproductive cycle during autumn, the presence of a primary corpus luteum regressed on the date of harvest can be used to describe temporal variation in timing of ovulation (cf. Langvatn *et al.* 2004 for details), which we refer to here as female phenology.

Population density

As an index for local density, we used total harvest (number of deer shot) in a municipality divided by the area of red deer habitat, as approved by the management authorities (Myrsterud *et al.* 2001c; Myrsterud *et al.* 2002). During the study period, the red deer population has been increasing steadily. The harvest has increased 10-fold (Statistics Norway 2004) and the number of deer killed in traffic has also increased, even after accounting for increase in traffic (Myrsterud 2004). We have found recently a close correlation between harvest size and independent indices of population size, such as the number of deer seen and population size estimated with cohort analysis (Myrsterud *et al.* 2007). This index of density also includes a spatial component, and may thus be affected potentially by habitat quality if resource levels for the same density differ. If such an effect was strong, it would probably yield a non-linear relationship between mass and density (or a poor fit). It emerged that the relationship between body mass and the density index was curvilinear if data from the municipality Eid were included. There were very few data from Eid, except from 2001 to 2003 (482 males and 379 females 1 year or older; only 27 individuals earlier than 2001). The deer harvested in Eid are mainly migrating deer shot on the way from their summer to winter ranges (Vebjørn Veiberg, personal communication). The density index for these deer may therefore be artificially high compared to the real densities they experience in their summer and winter areas. When excluding data from Eid, the relationship between body mass

and the density index did not deviate from linearity. We thus excluded data from Eid in all analyses.

Other covariates

As an index of global winter climate, we used the NAO (Hurrell 1995; Hurrell *et al.* 2003), which is known to have a strong impact of the life history of red deer along the South West coast of Norway (Myrsterud *et al.* 2001b; Pettoirelli *et al.* 2005). Because the data on body mass and ovulation cover a large area, and because not all sub-areas are sampled each year, it is important to control for factors with a known effect on body mass in order to avoid biased estimates. Several spatial covariates were therefore considered, including distance from the coast, degree of latitude, proportion of high altitude habitat and diversity of altitudes and aspects (Myrsterud *et al.* 2001a).

STATISTICAL ANALYSES

To estimate objectively the start of mass loss, peak of mass loss and end dates of mass loss, we applied threshold models (Ulm 1989; for an application see Lambin & Yoccoz 2001) with one or two breaking points (ϕ_1 , or ϕ_1 and ϕ_2 when ϕ_2 was estimable) on the predicted body mass from generalized additive model (GAM) fits (Hastie & Tibshirani 1990). Additive models were fitted using thin plate regression splines in the R library mgcv (Wood 2006; R Development Core Team 2007). Threshold breaks were discrete, as the covariate is Julian date. We did not aim here at finding a set of best models, as is conducted in other selection procedures, but simply at finding dates of changing slopes. For that reason, we considered only linear terms and did not attempt to fit models of higher order polynomial. The overall body mass loss of males before, during and after the rut was assessed by slopes of each segment of the piecewise regression. We replicated the same analysis on ovulation rates adjusting piecewise linear regressions of date on the predicted evolution of ovulation rate over time. We used piecewise regressions as a convenient tool for describing variation over time. Note, however, that for reading out predictions on proportions breeding, this requires logistic transformation (see Langvatn *et al.* 2004). We repeated this procedure of date estimation for each age class and for two density and NAO levels (greater or smaller than the study median) both for males and females.

Results

Adult females delayed start of ovulation by *c.* 5 days from low to high population density (Langvatn *et al.* 2004), implying a delay in the date of maximum ovulation rate at high compared to low density (Fig. 1; Table 2). Females also ovulated

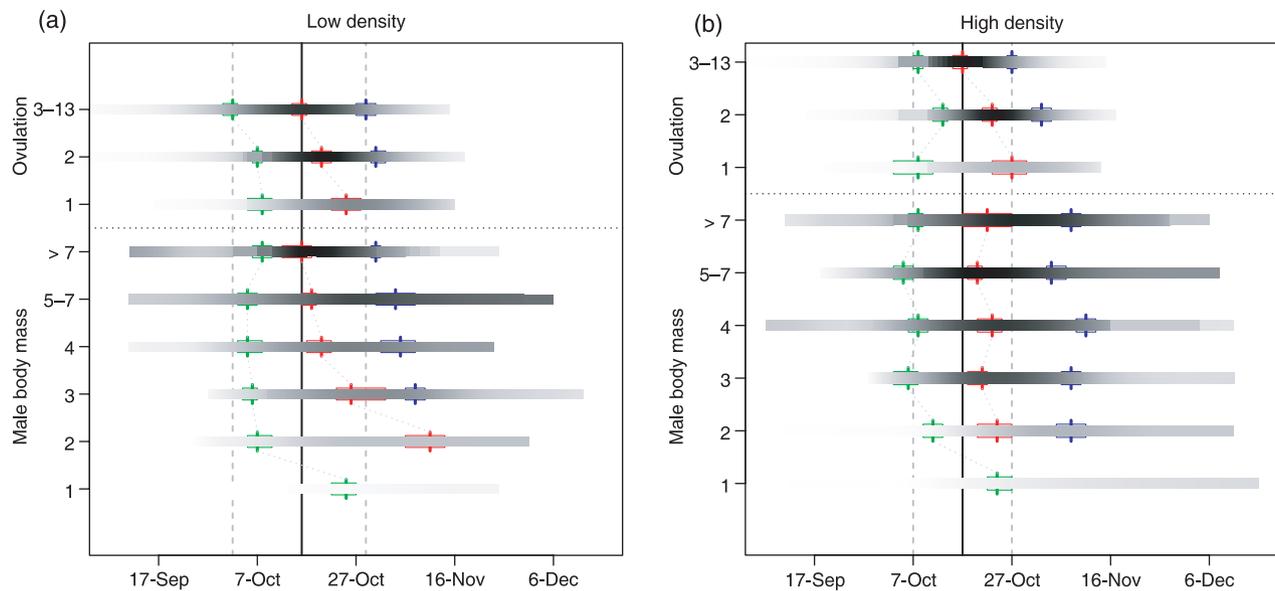


Fig. 1. Timing of male body mass decline and female ovulation at (a) low and (b) high density (relative to the median: 0.844 deer shot per km² 'deer habitat'). The six age categories for males are 1, 2, 3, 4, 5–7 and > 7 years, while the three female age categories are 1, 2 and 3–13 years. Dates for male mass loss and female ovulation were defined by the same threshold methods (see Methods). The vertical solid and dotted lines refer to peak and start/end dates of ovulation for females aged 3–13 years. The colour depth of the grey shaded bars refers to level of mass loss or ovulation rate. We provide bands for start (green), peak (red) and end (blue) of rutting. For some categories, we found no 'end dates' within the time span covered by our sampled material (until 15 November). The box surrounding bars represents the 95% confidence interval of the estimated dates.

Table 2. Timing of female ovulation at low and high density (relative to the median population density: 0.844 deer shot per km² of deer habitat). The three female age categories are 1, 2 and 3–13 years. For yearlings, we found no end dates within the time-span covered by our sampled material (until 15 November)

Age class	Start date (95% CI)	Max rate date (95% CI)	End date (95% CI)	Duration (days)
Yearlings				
Low	8 Oct (5 Oct; 10 Oct)	25 Oct (22 Oct; 28 Oct)	–	–
High	8 Oct (3 Oct; 11 Oct)	27 Oct (23 Oct; 30 Oct)	–	–
2 years old				
Low	7 Oct (6 Oct; 8 Oct)	20 Oct (18 Oct; 22 Oct)	25 Oct (21 Oct; 28 Oct)	24
High	13 Oct (11 Oct; 14 Oct)	23 Oct (21 Oct; 24 Oct)	2 Nov (31 Oct; 4 Nov)	20
3–13 years old				
Low	2 Oct (30 Sept; 3 Oct)	17 Oct (15 Oct; 18 Oct)	29 Oct (27 Oct; 31 Oct)	27
High	8 Oct (7 Oct; 9 Oct)	16 Oct (14 Oct; 17 Oct)	27 Oct (26 Oct; 28 Oct)	20

more synchronously at high than low density. In support of Hypothesis 1, that males track female phenology, peak body mass decline of all males older than 2 years were matching peak female ovulation at high density, but at low density only the prime-aged males did so (Fig. 1a; Table 2). At low density, both peak and end dates as well as total male effort over a rutting season (i.e. whole mass loss based on slope estimates, Table 3) were progressively earlier by increasing age (both absolutely and relatively, except for the very oldest ages classes; see Yoccoz *et al.* 2002). In contrast, starting dates of mass decline were similar in males 3 years or older and independent of

density (but note that overall mass loss differs depending on density; Yoccoz *et al.* 2002). At low density, male age groups were thus less synchronized in the peak and end dates of mass decline than at high density (Fig. 1), in support of Hypothesis 2. Indeed, at high density male age classes varied less with respect to timing of rutting effort and the observed sequence observed from young to old deer vanished (Fig. 1b; Table 3). As for female ovulation (Langvatn *et al.* 2004; Fig. 1), male body mass decline was not affected significantly by the NAO (Table 4), also in support of our Hypothesis 1. The GAM model with age class and date of harvest and their

Table 3. Development of male body mass before, during and after main rut in six age classes at high and low density. For each age class there is a linear increase in body mass (Slope₁) before a date (Threshold date₁), where body mass starts to drop (at the rate given in Slope₂). Threshold date₁ reflects the date where each age class starts to rut. In some age classes there is a second threshold (Threshold date₂), where mass loss levels out (Slope₃), i.e. the end of rut. As data after 15 November are scarce the second threshold is not detected in all age classes. Max refers to peak of rut. We repeated this procedure for high (above median) and low (below median) density and calculated the difference in slopes and threshold dates (low density–high density estimates). A positive difference in Slope₁ indicates less growth at high than low density prior to the most intensive rutting period. Negative differences between threshold dates indicate a delay in onset of rut at high compared to low density. Note that Slope₂ is less steep for the two youngest compared to older age classes, indicating little investment in rutting activities. Tabulated values are real estimates multiplied by 100

Age class	Slope ₁	Threshold date ₁ (95% CI)	Slope ₂	Threshold date ₂ (95% CI)	Slope ₃	Max (95% CI)
Yearlings						
Low density	0.051	13 Oct	-0.102	–	–	–
High density	0.015	13 Oct	-0.064	–	–	–
Difference (L–H)	0.036 (-72.2%)	0 day	-0.036 (+36.3%)	–	–	–
2 years old						
Low density	0.084	7 Oct (5 Oct; 10 Oct)	-0.174	–	–	–
High density	0.062	11 Oct (9 Oct; 13 Oct)	-0.136	8 Nov (5 Nov; 11 Nov)	–	25 Oct (21 Oct; 28 Oct)
Difference (L–H)	0.021 (-25.7%)	-4 days	-0.038 (+21.7%)	–	–	–
3 years old						
Low density	0.079	6 Oct (3 Oct; 7 Oct)	-0.416	8 Nov (6 Nov; 10 Nov)	–	27 Oct (24 Oct; 3 Nov)
High density	0.111	6 Oct (4 Oct; 7 Oct)	-0.430	8 Nov (6 Nov; 10 Nov)	-0.102	22 Oct (19 Oct; 23 Oct)
Difference (L–H)	0.031 (-28.7%)	0 day	0.013 (-3.2%)	0 day	–	5 days
4 years old						
Low density	-0.093	7 Oct (3 Oct; 8 Oct)	-0.482	–	–	21 Oct (18 Oct; 23 Oct)
High density	-0.128	8 Oct (6 Oct; 10 Oct)	-0.514	11 Nov (9 Nov; 13 Nov)	-0.142	24 Oct (21 Oct; 26 Oct)
Difference (L–H)	0.035 (-37.7%)	-1 day	0.031 (-6.6%)	–	–	-3 days
5–7 years old						
Low density	-0.266	5 Oct (3 Oct; 7 Oct)	-0.689	4 Nov (31 Oct; 8 Nov)	–	19 Oct (17 Oct; 20 Oct)
High density	-0.065	5 Oct (4 Oct; 7 Oct)	-0.601	4 Nov (3 Nov; 7 Nov)	-0.334	21 Oct (19 Oct; 22 Oct)
Difference (L–H)	0.200 (+75.4%)	0 day	-0.088 (+12.8%)	0 day	–	-2 days
> 7 years old						
Low density	-0.247	8 Oct (6 Oct; 9 Oct)	-0.824	8 Nov (7 Nov; 10 Nov)	-0.179	17 Oct (13 Oct; 19 Oct)
High density	-0.141	8 Oct (5 Oct; 10 Oct)	-0.550	31 Oct (30 Oct; 1 Nov)	-0.210	23 Oct (18 Oct; 28 Oct)
Difference (L–H)	0.106 (+42.9%)	0 day	-0.270 (+39.2%)	+9 days	–	-6 days

interaction explained 74% of the variance in body mass. The fit of the data to the model are presented in Fig. 2. The reported patterns were qualitatively consistent when analysis was replicated based only on population P3 (with most data), suggesting that temporal density dependence is operating (see Appendix SI in Supplementary material).

Discussion

The timing of breeding in strongly seasonal environments is a critical factor for reproductive success in large mammalian

herbivores which, at least in females, is well documented (Clutton-Brock *et al.* 1982; Loison, Langvatn & Solberg 1999; Holand *et al.* 2006). For males of a capital breeding species (*sensu* Jönsson 1997), we tested the hypothesis that timing of rutting effort would be a compromise between hitting peak female ovulation on one side (potential benefit) and avoiding investment of capital (fat) at the same time as superior contestants (costs). Indeed, we found that maximal daily mass loss of males followed changes in peak female ovulation, but that rutting phenology is more synchronous among age classes at high compared to low density. This is probably a

Table 4. Timing of male body mass decline at high and low values of the North Atlantic Oscillation (see Table 2 for definitions)

Age class	Start date (95% CI)	Max rate date (95% CI)	End date (95% CI)	Duration (days)
Yearlings				
High NAO	14 Oct (8 Oct; 31 Oct)	–	–	–
Low NAO	12 Oct (8 Oct; 15 Oct)	–	–	–
2 years old				
High NAO	7 Oct (5 Oct; 8 Oct)	22 Oct (18 Oct; 25 Oct)	–	–
Low NAO	10 Oct (8 Oct; 11 Oct)	26 Oct (22 Oct; 29 Oct)	9 Nov (3 Nov; 13 Nov)	31
3 years old				
High NAO	6 Oct (4 Oct; 8 Oct)	21 Oct (18 Oct; 23 Oct)	4 Nov (1 Nov; 6 Nov)	28
Low NAO	3 Oct (1 Oct; 5 Oct)	26 Oct (23 Oct; 28 Oct)	10 Nov (7 Nov; 13 Nov)	37
4 years old				
High NAO	6 Oct (4 Oct; 8 Oct)	24 Oct (21 Oct; 26 Oct)	11 Nov (9 Nov; 13 Nov)	35
Low NAO	7 Oct (5 Oct; 8 Oct)	20 Oct (18 Oct; 21 Oct)	5 Nov (2 Nov; 8 Nov)	28
5–7 years old				
High NAO	6 Oct (4 Oct; 7 Oct)	20 Oct (18 Oct; 22 Oct)	1 Nov (30 Oct; 3 Nov)	25
Low NAO	3 Oct (1 Oct; 4 Oct)	19 Oct (16 Oct; 21 Oct)	5 Nov (2 Nov; 9 Nov)	32
> 7 years old				
High NAO	7 Oct (6 Oct; 9 Oct)	17 Oct (12 Oct; 20 Oct)	4 Nov (3 Nov; 6 Nov)	27
Low NAO	4 Oct (3 Oct; 5 Oct)	21 Oct (17 Oct; 26 Oct)	30 Oct (28 Oct; 3 Nov)	26

consequence of lower competition among males, and thus intensity of sexual selection. With increasing density, female ovulation is more synchronous (Langvatn *et al.* 2004), male age structure is younger and the sex ratio is probably more female-biased (Milner *et al.* 2006), all contributing to changes in sexual selection intensity (see detailed discussion below). We also highlight that start, peak and end dates of rutting among age classes were not well correlated, making the start of rutting activities, in particular, a less useful measure of total rutting effort.

Longitudinal data on reproductive tactics spanning the range of ecological conditions necessary to address the issues raised here are currently not available, although clearly such data would be preferred due to potential problems with individual heterogeneity and hunter selectivity with transversal data such as ours. Harvesting data are often a selective sample of the population yielding a potential for bias (e.g. Martinez *et al.* 2005; Mysterud, Tryjanowski & Panek 2006). The important point is how strong such a bias is relative to the patterns of interest. In Norway, harvesting selectivity is regulated mainly with quotas, given as calf, yearling and adults of each sex. Based on our detailed experience with the system, it is unlikely that harvesting bias, i.e. selection for phenotypic traits such as body mass, is strong within these quota categories for this time-period. The hunting tradition is for meat, not for trophies (Milner *et al.* 2006). Also, there are

often large quotas and limited time for hunting, which reduce selectivity (Solberg *et al.* 2000). There is a high cost in terms of lost chances to be selective in the forested habitat along the West coast of Norway, where group size of red deer is small (average of 1.5 females per male in mixed groups during rut; Bonenfant *et al.* 2004). Potentially, mass loss during rut may be over-estimated if the largest males are harvested first. However, in these populations where the likelihood for a male to reach 4 years of age is < 10% (Langvatn & Loison 1999), any prime-aged male will appear very large. Thus, it is unlikely for hunters to select between a 'small' and a 'large' prime-aged stag, as in these populations prime-aged stags are so rare that if they appear and are legal to shoot, they will most probably be shot at the first encounter with a hunter. If such a bias was driving the pattern of male mass loss, we would also expect mass decay to be strong when hunting begins on 10 September until around the start of October, when rutting intensity increases. However, for this hunting period there is no or very slight mass loss (see Results). Indeed, some age classes increase in body mass before the rut starts, which cannot be explained by biased hunting. Thus, the pattern reported here cannot be explained by hunter selectivity. Also, the patterns of decay are probably not related to decreasing plant quality, as females start to have a negative energy balance much later (indicative of seasonality).

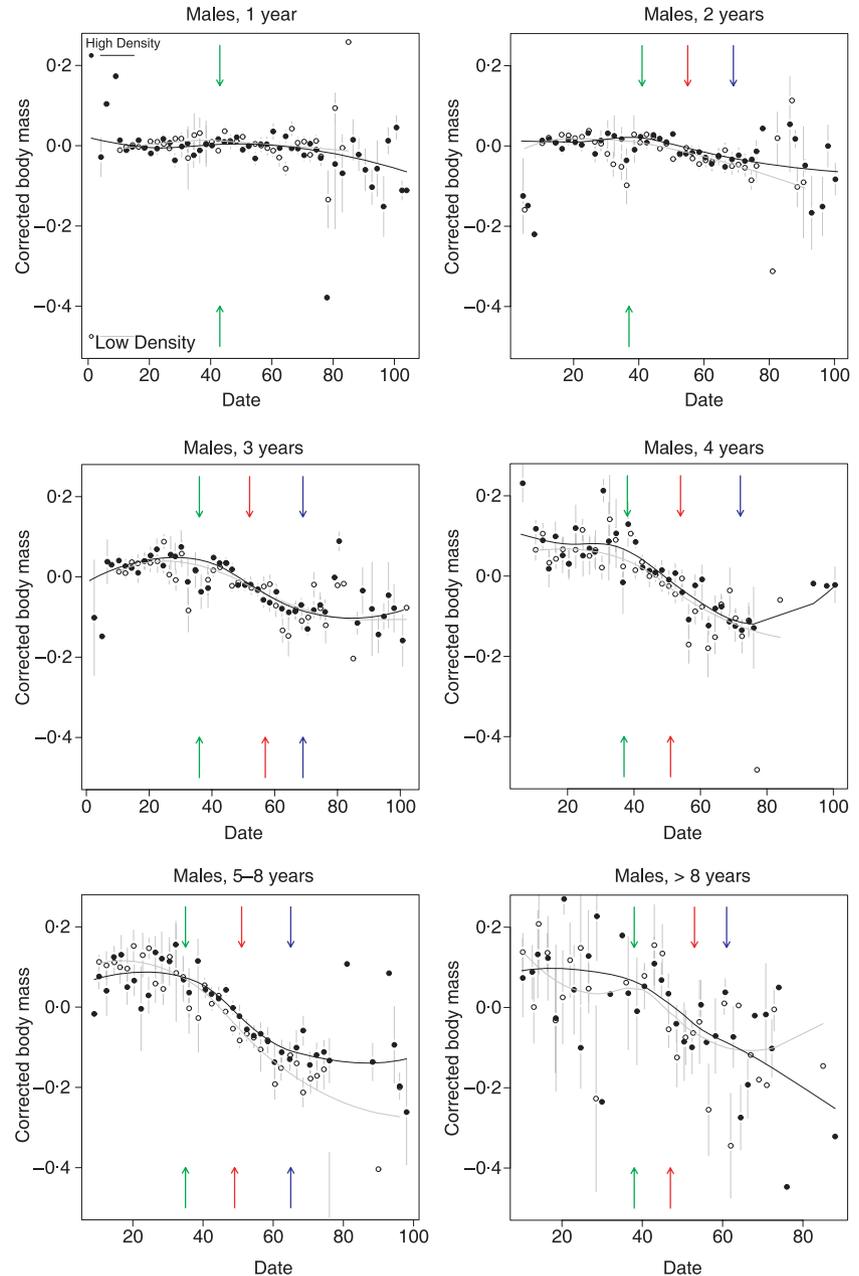


Fig. 2. Generalized additive model plots of corrected body mass against date of harvesting (counting days from 1 September) for each age class. Observations were pooled with a 2-day time-step. White with grey smoothed lines show data at high and low density values are shown in black with black lines. Threshold dates are indicated with arrows: start date (green), peak date (red) and end dates (blue). Arrows at the top are high density and arrows on bottom are low density.

In Soay sheep, males were shown to target their mate-guarding to the optimal insemination window of females (Preston *et al.* 2003). Our results are consistent with this, showing that the prime-aged males indeed time the maximal use of the capital to the period when mating is at stake (Fig. 1). The later peak mass decline in young males at low density indicates that they target their reproductive effort to the last part of the rut when most of the females have ovulated, when the capital of prime-aged males is becoming depleted. It may also be that prime-aged males are reluctant to invest more into the later parts of autumn due to increased chances of mortality during the subsequent winter (e.g. Toïgo & Gaillard 2003). The best evidence that late investment of young males is a successful strategy comes from the studies on Soay sheep showing increased paternity of younger males later in rut (Preston *et al.* 2001). While adult males deplete their fat

layers, subadults (in the presence of adult males) may even increase their fat layer throughout the rut due to low effort (Komers, Messier & Gates 1994; Mysterud *et al.* 2003). Yearling females, making up a substantial proportion of the population, are ovulating much later than prime-aged females. The prime aged males therefore seem to target mainly the older and heavier females ovulating early. The possibility that males are selecting for particular females has received little attention in the literature, but has been demonstrated in bison (*Bison bison*) (Berger 1989) and Soay sheep (Preston *et al.* 2005). Such issues may be particularly important in harvested populations with a skewed sex ratio.

Many aspects of the life history of ungulates in general is affected by harvesting (Mysterud, Coulson & Stenseth 2002). In our populations, sex ratios have become increasingly female-biased and the male age structure becomes younger with increasing density, due to heavy male-biased harvesting (Langvatn &

Loison 1999; Milner *et al.* 2006). Unfortunately, accurate information on sex ratio development is lacking. However, since 1978 the proportion of males in the adult harvest has been approximately 60% in Norway (Milner *et al.* 2006), resulting in female-biased populations with < 40% males in the adult segment. The average age of adult males (≥ 2 years) harvested has declined from 6.5 years in 1965 to 3.1 years in 2003 (population P3; A. Mysterud & R. Langvatn, unpublished information). In populations with a heavy male-biased harvest, young males may be more involved in rut when few prime-aged males are present than in non-harvested populations (Komers *et al.* 1994; Mysterud *et al.* 2003). Indeed, we found that even young red deer males decline in body mass during rut (Yoccoz *et al.* 2002; this study), but much less than prime-aged males. The maximum daily mass loss for Norwegian red deer males during rut was 0.1, 0.3, 0.6, 0.7, 0.9 and 1.0% for, respectively, yearlings, 2-year-olds, 3-year-olds, 4-year-olds, 5–7-year-olds and more than 7-year-olds. Note, however, that the relationship between effort and reproductive success in males is complicated by differences in individual quality (McElligott *et al.* 2003; Pelletier 2005; Pelletier *et al.* 2006).

In addition to increasingly female-biased sex ratios and younger male age structure with increasing population density, there is another independent process that can also decrease the level of male competition. The ovulation period is more synchronized at high density than at low density (from 10 to 80% in 13 days at high vs. 21 days at low density; Langvatn *et al.* 2004). Thus, depending on the male's ability to gather and defend females, and hence on female spatial distribution (Jarman 1974; Emlen & Oring 1977), a high number of receptive females at the same time may decrease the chances of dominant males to monopolize all females. In our Norwegian populations females live in small scattered groups, averaging only 1.5 females per male in mixed groups during rut (Bonenfant *et al.* 2004), and monopolizing many synchronized females at the same time is unlikely for a single male. Both these patterns can thus relieve the intensity of sexual selection processes with increasing density (Wade, Shuster & Demuth 2003; Wade & Shuster 2004). Consistent with such a scenario, male age groups were indeed more synchronized in their peak decay at high density, suggesting that males of different ages were more able to mate successfully during peak rut at high density (see also Coltman *et al.* 1999 on Soay sheep). This provides evidence for the suggestion that male rutting phenology in capital breeders is best interpreted as a compromise between hitting peak female ovulation and the level of sexual selection forces that may change with population density. Such a lowering of sexual selection forces may, in turn, lead to a higher effective population size, if a higher proportion of males gain successful mating (Hard, Mills & Peek 2007).

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Temporal vs. spatial density dependence

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2008.01365.x>
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