Age-specific feeding cessation in male red deer during rut

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Abstract

Tactics for resource-use involve both using stored reserves (capital breeding) and feeding while reproducing (income breeding). In polygynous ungulates, males often use an income breeding strategy when young and shift to a capital breeding tactic at prime age. Little is known regarding why prime-aged males stop or largely reduce eating during rut but still remain inactive for as much time as before rut. A detailed exploration of how rumen content correlates with age and date may shed light on the ultimate causes of why some males stop eating. We provide quantitative empirical data on rumen content from red deer Cervus elaphus during the rutting season in Norway. In male red deer, rumen content declined with age, up to around 6 years of age. Above this age, rumen content was low and stable. A time-of-year effect on rumen content was best described with a second-order polynomial term, as rumen fill was lowest during mid-October when the mass loss of males and the ovulation rate of females both peak. We present two new hypotheses related to why males reduce eating (physical rest and parasite hypotheses). Two related patterns need to be explained and better documented: (1) why are resting times stable before, after and during rut, and (2) why do non-prime-aged males eat more between rutting activities?

Introduction

Reproduction is energetically costly (Reznick, 1985; Reznick, Nunney & Tessier, 2000). Different tactics to acquire resources for reproduction depend on environmental or individual conditions (Bonnet et al., 2002; Lourdais et al., 2002). For long-lived species, individual tactics also vary with sex and stage of development (Mysterud, Solberg & Yoccoz, 2005). Tactics of resource use for reproduction can be categorized along the capital-income breeding continuum, depending on the type of resources allocated to reproduction (Stearns, 1992; Jönsson, 1997). In highly polygynous species such as many cervids, males are usually regarded as capital breeders, meaning the energy allocated to reproduction derives from stored reserves during the preceding spring and summer (mainly fat). Younger males do not always rut, but they do so in many harvested populations with a young age structure. However, younger males follow an income breeding strategy; that is, the energy allocated to reproduction comes from available resources at the time of rutting (red deer Cervus elaphus: Clutton-Brock, Guinness & Albon, 1982; reindeer Rangifer tarandus: Kojola, 1991; moose Alces alces: Miquelle, 1990; bison Bison bison: Maher & Byers, 1987; Komers, Messier & Gates, 1994; mouflons Ovis gmelini: Bon et al., 1995; Dall sheep Ovis dalli: Singer et al., 1991; review in Mysterud, Langvatn & Stenseth, 2004). The fact that young males still forage and eat may be because they are excluded from rut by older males and thus put resources into body growth (Mysterud et al., 2003).

Few ultimate hypotheses have been advanced as to why males stop feeding during the rut. Why is it beneficial to stop (or largely reduce) eating in order to increase fitness, if getting more energy increases fitness? Males reduce levels of feeding when rutting activities increase (Mysterud et al., 2004; Willisch & Ingold, 2007), but why do they remain inactive when they could be feeding or ruminating? Indeed, inactive time is constant before, during and after rut, so rutting activity is at the cost of feeding time (Willisch & Ingold, 2007). Why rest so much? Recently, the energy-saving hypothesis (Willisch & Ingold, 2007) was proposed to explain this paradox. The argument is that males might be unable to maintain the basic cyclic pattern of ingesting and ruminating food during rut, because when effective digestion cannot be maintained during the rut, shifting to an energy-saving strategy may become advantageous. Foraging requires energy for searching, which is not compensated by digestion (Willisch & Ingold, 2007). The energy-saving hypothesis would predict threshold effects: under a certain level of foraging, the regular feeding-rumination rhythm breaks down. A threshold is expected for male age at the first year of full involvement in reproduction, as reproductive costs would lead to the onset of mass loss.

Here, we assess feeding activity with rumen content from red deer harvested during the rutting season in Norway. We test whether (P_1) prime-aged males feed less than younger males during rut, and explicitly test for the two alternatives that (P_{1a}) a linear relationship or (P_{1b}) a (non-linear) threshold-like relationship exists between rumen content and age. Regarding date and rumen content, the rutting effort of males, as measured by somatic mass loss, peaks when most females are ovulating (Mysterud *et al.*, 2008). We thus test for a similar (P_{2a}) gradual decrease and then increase in rumen content around this peak (i.e. second-order polynomial). Alternatively, either (P_{2b}) a stable, low rumen fill could occur during rut, or rumen fill could decline by rutting date as a result of reduced availability of high-quality forage as autumn progresses (i.e. first-order linear relationships). Individual condition is important for mass loss, that is, heavy males lose relatively more weight than light males (fallow deer *Dama dama*: McElligott *et al.*, 2003; bighorn sheep *Ovis canadensis*: Pelletier, 2005); thus, (P_3) males of larger size may eat less than smaller males. To control for possible seasonal effects on forage intake, we compared age and date patterns of male rumen content with female rumen content. For females, we predict (P_4) no age effect and (P_5) a seasonal decline in rumen fill not related to peak rut.

Material and methods

Study area

The data originate from the Songli Research Station (8000 ha; 63°20′N, 9°39′E) in Orkdal municipality, situated in the inland of Sør-Trøndelag county, Norway. The natural vegetation is dominated by open pine forest *Pinus sylvestris* with juniper *Juniperus communis*, heather *Calluna vulgaris* and bilberry *Vaccinium myrtillus* (Albon & Langvatn, 1992). The terrain is hilly, but flatter areas have been cleared for agricultural use and are often used by red deer. The climate is cold with snow for 4–5 months, and the deer migrate to lower elevations during winter (Albon & Langvatn, 1992). The density of red deer has increased over time, as evidenced from the harvest records and other independent indices (Mysterud *et al.*, 2007), with 11 deer harvested in 1959 and 175 in 2001 for the municipality of Orkdal (Statistics Norway, 2004).

Red deer data

Data on mass of rumen content, body mass, jawbone size, sex, age and date of harvest were obtained from 81 male and 38 female red deer sampled over the years 1959–1979 and the year 2001. Data derive from hunting on the property of the research station. Body mass is dressed mass (i.e., live mass minus head, skin, viscera, bleedable blood and metapodials). Dressed mass is about 58% of live mass (Langvatn, 1977) and is highly correlated with total mass in cervids (Wallin, Cederlund & Pehrson, 1996). Age determination in calves and yearlings was based on tooth eruption (Loe *et al.*, 2004); older animals were aged using annuli in the cementum

of the first incisor (Hamlin *et al.*, 2000). Lactation status was deduced by the presence of milk, which is present until December/January (Clutton-Brock *et al.*, 1982). Only ≥ 1-year-old deer shot between 20 September and 31 October were included, as this is the main rutting season in Norway (Yoccoz *et al.*, 2002; Loe *et al.*, 2005; Mysterud *et al.*, 2008).

Statistical analysis

We used mainly linear models (McCullagh & Nelder, 1989) to analyse the relationship between our response variable rumen mass and the predictor variables. What we term a date effect is a date in autumn modeled as a continuous variable, starting with day 1 on 1 September. Rumen mass was ln-transformed before analysis to obtain a normal distribution of the data. We first tested for a jaw length effect on rumen content to account for potential allometric relationships between body size and rumen mass. We predicted non-linear effects of age and date, as was also suggested graphically by exploratory use of additive models (Wood, 2006; results not shown). We therefore compared the fit of several parameterizations that mimic different types of biologically motivated non-linearity. More specifically, we tested predictions by respectively fitting and comparing polynomials (second order) and threshold models. A possible advantage of the threshold model is that it allows for a flat effect of age, for example within the prime-aged individuals, while having a linear increase or decrease for younger or very old animals. When using a threshold effect, we iteratively fitted threshold functions (with one breaking point, ϕ_1) while minimizing the residual sum of squares (analogous to using profile likelihood; Ulm, 1989) to estimate the age or date when rumen fill dropped (or increased) suddenly (Lambin & Yoccoz, 2001; Loe *et al.*, 2005). All analyses were conducted for each sex separately. To control for possible between-year variation in onset of rutting, we included a density index (no. of harvested deer per km^2 of red deer habitat), known to be linked to slightly delayed onset of ovulation in females (Langvatn *et al.*, 2004). Model selection was based on the information theoretic approach (Burnham & Anderson, 2002). We chose the Akaike's Information Criterion corrected for sample size (AIC$_c$) as the selection criterion, given our relatively small sample size. All computations were performed with R 2.6.0 (R Development Core Team, 2006).

Results

The rumen content of male red deer decreased markedly up to the age of around 6 years. After this age, rumen fill was stable and low (Fig. 1b). A threshold effect for age provided the best fit to the data ($r^2 = 0.57$, Supplementary Material Table S1), consistent with P_{1b}. Mass of rumen content decreased in the first period of the rut, but was then fairly stable (and low) for the rest of the rut (Fig. 1a). The best model included the effect of date as a second-order polynomial term (Supplementary Material Table S1), and rumen content was lowest around 15 October (Fig. 1b), consistent with P_{2b}. However, we found no clear evidence of an interaction between age and date effects, although the non-
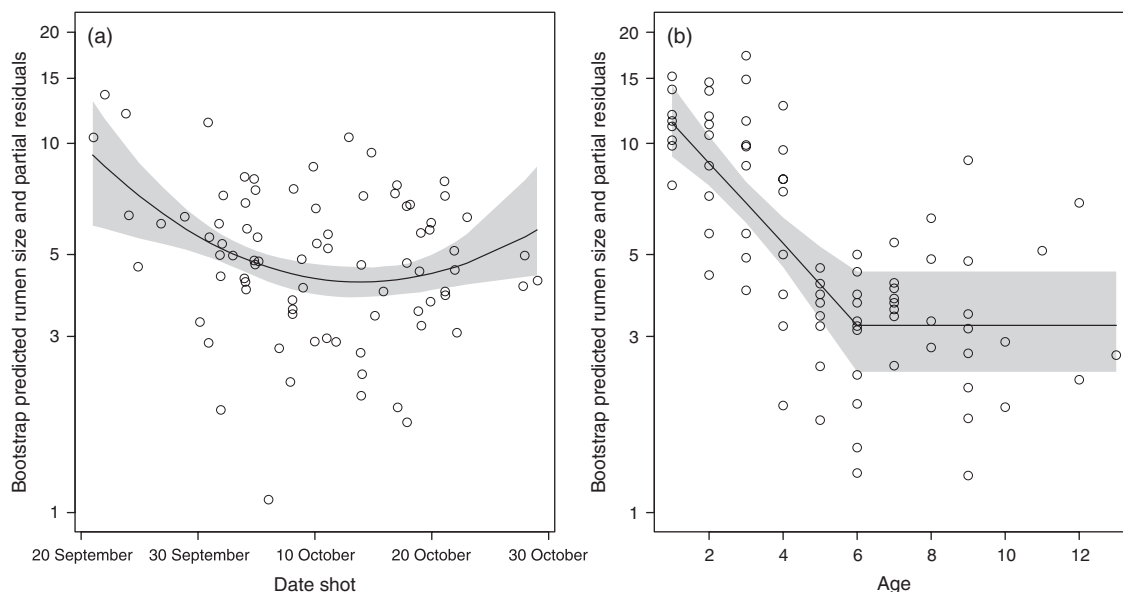
Figure 1 Relationship between rumen mass (kg) and (a) date and (b) age of male red deer *Cervus elaphus* during autumn in Orkdal, Norway ($r^2 = 0.57$). A threshold model for age provided the best fit to the data (Supplementary Material Table S1). The dataset was too limited to separate possible interactions between date and age effects. The grey shading represents the 95% confidence limits, for model predictions of the mean are calculated robustly using bootstrapping.

Table 1 The parameter estimates for the best models (Tables 1) for (ln) rumen fill in (A) male ($n=81$) and (B) female ($n=38$) red deer *Cervus elaphus* in Norway during autumn rut

	Estimate	Standard error	*t*	*P*
(A) Males				
Intercept	5.3527	1.0080	5.310	0.000
Date of harvest	−0.1226	0.0543	−2.257	0.027
Date of harvest^2	0.0014	0.0007	2.027	0.046
Age 1–6 years	−0.3091	0.0418	−7.403	0.000
Age ≥ 6 years	0	0		
Density	0.2450	0.4080	0.601	0.550
(B) Females				
Intercept	2.806	0.188		
Lactating versus Yeld	0.254	0.078	3.232	0.002
Date of harvest	−0.010	0.004	−2.299	0.027

significant estimate was in the predicted direction (weaker date^2 effect in younger males). A negative effect of body size on rumen mass (P$_3$) after accounting for age and date of shooting was not evident, that is, heavy males within a given age class did not suppress feeding to a higher extent than lighter males (estimate: mean = 0.326, SE = 1.470; Supplementary Material Table S1). Although the effect of density entered the best model, it was not significant when the most parsimonious model was parameterized (Table 1).

The pattern of rumen fill in females was different. Rumen mass in females was related to lactation status but not to age *per se* ($r^2 = 0.34$, Supplementary Material Table S1), although the two are correlated. A significant linear decrease in rumen content occurred with date of harvest in
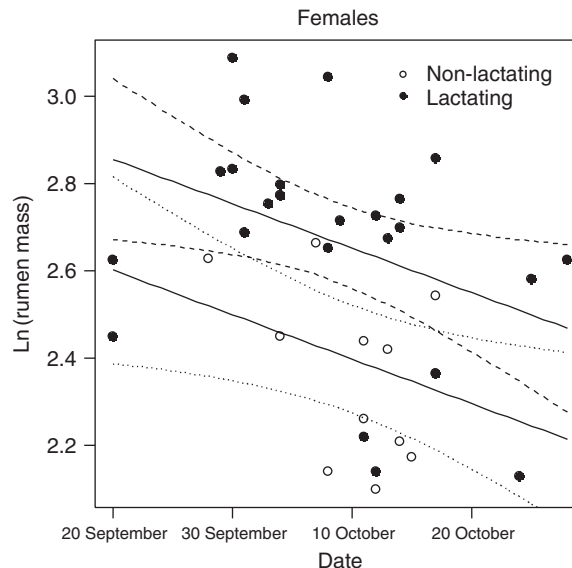

Figure 2 Rumen fill (kg) in lactating and non-lactating female red deer *Cervus elaphus* in Orkdal, Norway ($r^2 = 0.34$). Only 2- and 3-year-old females showed variation in lactation status. One-year-olds were not lactating while all females 4 years or older (with the exception of one 6-year-old) were lactating. An increased energy requirement among lactating hinds remains the most likely mechanism for the higher degree of rumen fill, as the effect of lactation remained significant after age was accounted for. The grey shading represents the 95% confidence limits, for model predictions are calculated robustly using bootstrapping.

females (Fig. 2, Table 1), indicating a seasonal decline in plant quality, metabolism and appetite (P$_5$), but the decrease

was not related to peak of rut. The effect size (i.e. slope estimate) of date was much smaller for females than for males (Table 1). The sex-specific pattern of rumen fill during autumn indicates that rumen mass in rutting males declines more than expected from seasonality alone.

Discussion

Prime-aged males in highly polygynous ungulates spend all of their fat reserves in a few short weeks during rutting in autumn, while younger males that are still growing lose much less stored reserves during rut. This age-dependent mass loss is caused by a corresponding age-dependent cessation of feeding (Mysterud *et al.*, 2004). Details in the pattern of how rumen content varies with age and date can shed light on the ultimate causes of why adult males stop (or largely reduce) eating during rut.

Threshold versus linear effects

Younger males have a lower likelihood of immediate reproduction when competing with larger males and, therefore, give a higher priority to growth in order to increase future chances of reproduction. The youngsters lose little or no mass during rut (Yoccoz *et al.*, 2002; Mysterud *et al.*, 2005), and our results clearly show that they indeed have filled rumens. What are the potential benefits of cessation of eating by prime-aged males? According to the energy-saving hypothesis (Willisch & Ingold, 2007), the prime-aged males most involved in rutting stop eating because efficient digestion is not possible with the limited time available for feeding. Consistent with predictions from the energy-saving hypothesis (P_{1b}), we found a steep decline in feeding up to an age of around 6 years in male red deer (Fig. 1a). Above this age, males have low rumen content, indicating that they allocate most time to other activities at the cost of foraging. However, the date effect on rumen content was best described as a second-order polynomial term, although scatter was large (Fig. 1b). The rumen fill over time had the lowest level, matching the time when the mass loss of males (Mysterud *et al.*, 2008) and ovulation rate of females both peak for red deer in Norway (Langvatn *et al.*, 2004). As passage through the digestive system takes about 2–3 days, some low level of feeding may occur during the more peripheral time periods of rut, and the transition is not abrupt as predicted in the energy-saving hypothesis.

Two related patterns need explanation: (1) why are resting times stable before, after and during rut, and (2) why do non-prime-aged males eat between their rutting activities? The energy-saving hypothesis addresses the latter question. We propose an alternative hypothesis, *the physical rest hypothesis*, and suggest that physical rest of muscles is necessary to successfully compete for access to females. Thus, time for muscle rest constrains time for feeding, given that active time is devoted to rut-related activities. The physical rest hypothesis predicts more linear effects between time devoted to rutting and rumen fill because, according to this hypothesis, a lower limit to time spent foraging does not result from the digestive

system. At present, both the physical rest and the energy-saving hypotheses have some support, as each fits the date and age effects, respectively. Also, more than one process may occur.

Perhaps the date effect should only be tested for prime-aged males that do stop eating? In our models, we pooled date effects for males of different age classes, because the interaction term between age and date effect did not enter the best model. However, when estimated, the tendency was a stronger date effect in prime-aged males than in younger males (Fig. 1b). For red deer in Poland, a figure reporting the date effect on the rumen content of only adult males showed an even more marked decline followed by increase in fill (Bobek, Perzanowski & Weiner, 1990). Therefore, as the pattern was similar and even clearer, being able to estimate the age and date interaction would not change our conclusion of supporting P_{2a}. Further, we have only indirectly controlled for between-year variation in onset of rutting by including a density index related to delayed ovulation in autumn (Langvatn *et al.*, 2004). Nevertheless, we cannot fully exclude the possibility that inclusion of data from several years makes detecting a threshold effect of date more difficult, particularly if the density effect interacts with other factors.

Further hypotheses required?

The two hypotheses discussed above are not the only possible ultimate explanations for why some males stop eating. Increasing attention is being paid to the link between foraging and disease (Hall *et al.*, 2007). We propose a *parasite hypothesis*, suggesting that due to a reduced immune system during rutting, males most involved in rutting may avoid eating because they are less able to fight parasites ingested during feeding. This would be another attempt to understand why prime-aged males do not eat between rutting activities. This parasite hypothesis is an extension of a more general hypothesis: that voluntary food intake drops during parasitic infections. The parasite hypothesis assumes a trade-off between investing in the immune system and in reproduction (Kyriazakis, Tolkamp & Hutchings, 1998). In bighorn sheep, parasite infection peaked for males during the rutting period and for females during the late gestation and lactation period (the periods of most heavy investment in reproduction; Pelletier & Festa-Bianchet, 2004; Pelletier *et al.*, 2005). In this case, reduced feeding during rut was due to increased activity of parasites already present within the host and not related to ingestion of new ones, but the case shows that parasites may be important. More detailed information regarding the functioning of the immune system over time for different age classes of males would be required to derive clear predictions from this hypothesis. In sum, our study highlights how detailed predictions of linear and non-linear relationships can yield insight into the ultimate causes of feeding cessation of male ungulates during rut.

Acknowledgements

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Supplementary material

The following material is available for this article online:

Table S1. The alternative models for (ln) rumen fill in a) male ($n = 81$) and b) female ($n = 38$) red deer in Norway during autumn rut. The column k refers to number of parameters and ΔAIC_c to the difference in AIC_c with the best model; w_i is the AIC_c weight and gives the relative likelihood that the ith model is the best model describing our data relatively to the other models used. ageT1 = effect of age from 1–5 years of age; ageT2 = effect of age for > 5 years of age. When ageT2 do not enter but ageT1 does, then the estimate for ageT2 = 0 (cfr. Fig. 1).

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