Age- and density-dependent reproductive effort in male red deer

Nigel G. Yoccoz[1,2]**, Atle Mysterud**[1]**, Rolf Langvatn**[3] **and Nils Chr. Stenseth**[1*]

[1]*Department of Biology, Division of Zoology, University of Oslo, PO Box 1050 Blindern, N-0316 Oslo, Norway*
[2]*Department of Arctic Ecology, Norwegian Institute for Nature Research, Polar Environmental Centre, N-9296 Tromsø, Norway*
[3]*University Courses on Svalbard, N-9170 Longyearbyen, Spitsbergen, Norway*

Reproductive effort in female ungulates originates from gestation and lactation and has been studied extensively; however, no comparable studies of reproductive effort in males (due to fighting for access to mates) have, to our knowledge, previously been reported. Here, we report on weight loss of male red deer during the annual mating season—a direct measure of male reproductive effort (or somatic reproductive costs). The 'terminal investment' hypothesis predicts that reproductive effort should increase with age, given that costs remain stable. We also propose the 'mating strategy-effort' hypothesis, which predicts that reproductive effort peaks in prime-aged males, since they are most often the harem holders. Consistent with the mating strategy-effort hypothesis, relative weight loss during the rutting season peaked at prime age and was lower in younger and senescent males. Weight loss during the rut was relatively smaller as density increased and more so for older males. This is probably primarily due to males (particularly senescent males) starting their rut in poorer condition at high density. The pattern of reproductive effort in males with regard to age and density therefore differs markedly from the pattern reported for females.

Keywords: body weight; *Cervus elaphus*; cost of reproduction; mating system;
terminal investment hypothesis

1. INTRODUCTION

Charles Darwin taught us that sexual selection arises from differences in reproductive success caused by competition over mates, which have led to different evolutionary trajectories of the sexes (Darwin 1871). Reproductive success in male red deer (*Cervus elaphus*) and most other dimorphic mammals depends on fighting with other males for access to mates (Clutton-Brock *et al.* 1982; Geist 1986; Gosling *et al.* 1987; Festa-Bianchet *et al.* 1990; Komers *et al.* 1994), whereas reproductive success in females depends on raising young successfully (Clutton-Brock *et al.* 1988). Reproductive effort in females is therefore made during gestation and lactation and has been studied extensively (Clutton-Brock *et al.* 1989); to our knowledge, no comparable studies of reproductive effort have been done for males.

A central concept in life-history theory is that there often is a trade-off between current reproductive effort and future fecundity and survival (Stearns 1992). Many species of large mammals are thought to rely heavily on accumulated body reserves to satisfy the energy needs of reproduction and survival (Festa-Bianchet *et al.* 1998)—they are so called 'capital breeders' (Stearns 1992; Jönsson 1997). Phenotypic correlations are thought to provide a good assessment of the cost of reproduction in large herbivorous mammals in which experimental manipulation of reproductive effort is difficult (Festa-Bianchet *et al.* 1998). Trade-offs between reproductive effort and body growth

or condition of females are well documented (Green & Rothstein 1991; Sand 1998). However, it is difficult to measure the effect of reproductive effort directly on body weight in males, as repeated measures of body weight are usually not possible in the field. Surrogate measures, such as frequency of fights (Clutton-Brock *et al.* 1982; Alvarez 1993; Pélabon *et al.* 1999) or level of other rutting activities, are difficult to interpret, not least because prime-aged males in general are better than younger males at fighting and costs are, as a result, highly asymmetrical (Clutton-Brock *et al.* 1982). Comparison of the activity budgets of young and prime-aged males suggests a higher reproductive effort in prime-aged males in the moose, *Alces alces* (Miquelle 1990) and the bison, *Bison bison* (Maher & Byers 1987). Consistent with this, on very limited datasets, a higher weight loss during rut was found for prime-aged males compared with young males in the red deer (Dzieciolowski *et al.* 1996; see also Bobek *et al.* (1990) for prime-aged males) and reindeer, *Rangifer tarandus* (Kojola 1985).

The pattern of reproductive effort over ages is most commonly used to test the 'terminal investment' hypothesis, though investment refers to parental effort relative to costs (Evans 1990). Observations in female ungulates so far seem consistent with the terminal investment hypothesis (Clutton-Brock 1984; Ericsson *et al.* 2001), which predicts increasing investment with age as residual reproductive value decreases (Williams 1966; Pianka & Parker 1975). However, data on old, senescent males are generally unavailable but are crucial for testing the terminal investment hypotheses. These old males are often not able to defend a harem (Clutton-Brock *et al.* 1982) and we
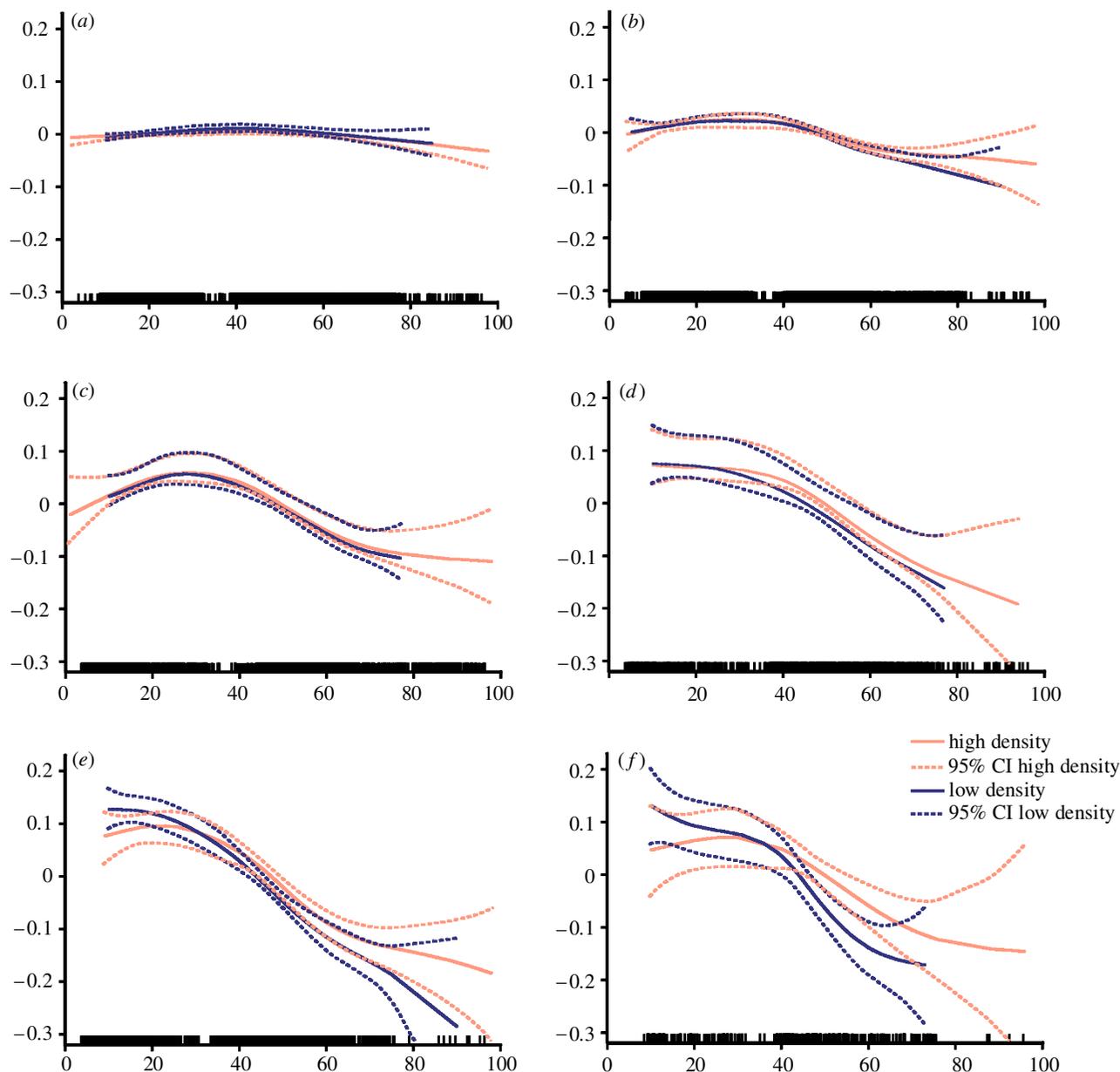
*Author for correspondence (n.c.stenseth@bio.uio.no).

Proc. R. Soc. Lond. B (2002) **269**, 1523–1528
DOI 10.1098/rspb.2002.2047

1523

© 2002 The Royal Society

Figure 1. The relationship between body weight of red deer males of different age classes. (*a*) One-year-olds; (*b*) two-year-olds; (*c*) three-year-olds; (*d*) four-year-olds; (*e*) five- to seven-year-olds; (*f*) older than seven-year-olds; and date of culling (an index for weight loss during rut) at high and low density along the west coast of Norway, presented as a result of fitting an additive model to the red deer data on body weights with smooth functions on continuous predictor (test statistics are given in electronic Appendix A). The tick marks show the locations of the observations on that variable (Venables & Ripley 1994).

may expect that reproductive effort is higher among harem holders. We call this the 'mating strategy-effort' hypothesis, which predicts that reproductive effort peaks in prime-aged males. Furthermore, there is little information available on how density affects reproductive effort in males. Both increased (fallow deer, *Dama dama*; Alvarez 1993; Pélabon *et al.* 1999) and decreased (red deer; Clutton-Brock *et al.* 1982) frequency of fighting with increasing density has been reported in ungulates. No study, to our knowledge, has tested for density-dependent reproductive effort directly on body weight loss, nor assessed the possible interaction between age and density. Using a unique dataset on body weight of 13 913 male red deer harvested at various stages of the rut along the west coast of Norway, including all age-classes up to 19 years of age (see electronic Appendix A, table A1,

available on The Royal Society's Publications Web site) and the years 1975–1999, we assessed age- and density-related changes in reproductive effort (somatic cost of reproduction). Our analysis adds to the understanding of the different evolutionary trajectories of the sexes originally suggested by Darwin (1871).

2. MATERIAL AND METHODS

(a) *Red deer data*

The data derive from 105 municipalities in six Norwegian counties on the west coast of Norway; a detailed description of the data is given elsewhere (Mysterud *et al.* 2001*a*,*b*,*c*). Data on dressed weight together with records of date of culling, teeth (for age determination; Hamlin *et al.* 2000) and locality (municipality) of 13 913 male red deer were sampled during the
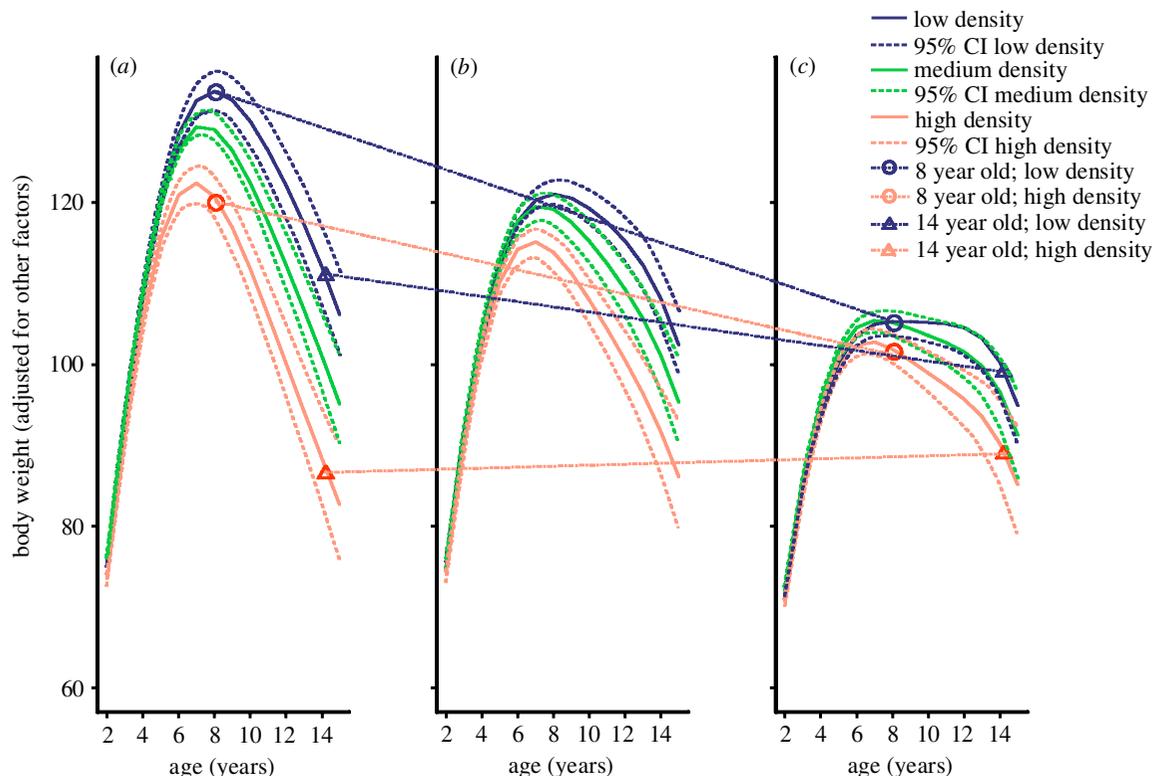
Figure 2. The relationship between body weight and age presented at different stages of the rut; (*a*) pre-rut; (*b*) mid-rut; (*c*) post-rut; and for three different densities. The predicted values of weight are plotted, all variables other than age, density and date of culling being taken as equal to their mean value. The curve corresponds to population P3 = Møre and Romsdal and Sør-Trøndelag counties; similar curves are observed in other populations. For young males density has little effect on weight loss during the rut. Whereas prime-aged males enter the rut in poorer condition at high than at low density, the effect of density at the end of the rut is much weaker. This contrasts with the oldest male age groups in which the effect of density is also much more persistent after the rutting period, while the overall weight loss during the rut was low.

annual autumn harvest 1975–1999 (Mysterud *et al.* 2001*b,c*). Red deer may only be shot between 10 September and 15 November, which includes the entire rutting period for red deer in Norway. Therefore, when regressing body weight against 'date of culling', the slope for the variable 'date of culling' estimates weight loss during the rutting season.

(b) *Statistical analyses*

We used a combination of linear models (LMs) and additive models (AMs) (Hastie & Tibshirani 1990) for statistical analyses. LMs were used for model selection, as interactions and parameter estimates have an easy interpretation, here. AMs were used to assess whether relationships were adequately fitted using LMs. A logarithmic transformation [ln(weight)] of body weight resulted in residuals with constant variance. By doing a logarithmic transformation of body weight, analysis of weight changes is seen on a relative scale, i.e. that differences between, for example, young and prime-aged males in the analysis are not due to differences in initial weight.

We identified the combination of variables giving the most parsimonious model for variation of body weight using Akaike Information Criteria (Burnham & Anderson 1998). As the effect of some variables is nonlinear, for example, age (Mysterud *et al.* 2001*c*) and the North Atlantic Oscillations (NAOs) (Mysterud *et al.* 2001*b*), we used polynomials to describe nonlinear relationships. We did not rely on 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 polynomial may not. We therefore systematically explored mod-

els with high-order polynomials, at least up to a fifth order. Covariates found in earlier studies of the Norwegian red deer were included. These were: age (Mysterud *et al.* 2001*c*); density (Mysterud *et al.* 2001*c*); cumulative density of the last 10 years prior to harvest (Mysterud *et al.* 2001*a*); the NAO (Mysterud *et al.* 2001*b*); distance from the coast (Mysterud *et al.* 2001*a*); degree of latitude (Mysterud *et al.* 2001*a*); diversity of altitudes; diversity of aspects; proportion of high-altitude habitat (Mysterud *et al.* 2001*a*) and the categorical variable population (P1, Rogaland and Hordaland counties; P2, Sogn and Fjordane county; P3, Møre and Romsdal and Sør-Trøndelag counties; P4, Nord-Trøndelag county; P5, the island Hitra) (Mysterud *et al.* 2000; Mysterud *et al.* 2001*b,c*). Interactions between population and age, and between population and the NAOs, were included.

We standardized the predictor variables, date of culling and density (mean 0, variance 1) to facilitate the interpretation of the interaction terms (Mysterud *et al.* 2000). The coefficient for a variable is then the strength of this variable when the other variables are at their average values (because the interaction terms are then zero). To assess the interaction between date of culling and age (to test for age-dependent reproductive effort), density and date of culling (to test for density dependence in reproductive effort) and density and date of culling and age (to test for age-dependent density dependence in reproductive effort), we restricted the analysis to multiplicative terms (denoted as, respectively, age × density, density × (date of culling), age × density × (date of culling)). Polynomials were also included in the interaction terms. Running simpler models with

fewer interactions included did not change the conclusions presented (see electronic Appendix A).

3. RESULTS

A somatic cost of reproduction during the rutting season was found for all adult age classes (figure 1; $R^2_{(full\ model)} = 0.770$; see electronic Appendix A); females lose no weight during the same period (Mysterud *et al.* 2001*c*). Male weight loss during the rutting season increased markedly with age until prime age was reached (figure 1); young males lost very little weight (figure 1*a*). After prime age, weight loss during the rut declined with advancing age (figure 2). Weight loss during rut was higher at low than at high density, and more so in old, senescent males (figure 2). Note also that weight before rutting started was much lower at high density, whereas there was little difference in weight due to density after the rutting season was ended (figure 2).

4. DISCUSSION

That weight loss is the least in young and senescent males, neither of which may be able to defend a harem, supports the mating strategy-effort hypothesis. Accordingly, there is no support for the terminal investment hypothesis, given that mortality increases similarly with weight loss for all age classes. This pattern suggests that harem holders incur a greatly increased somatic cost of reproduction compared with a 'sneaker' strategy. Corroborative evidence that weight loss during the rut is closely related to the mating strategy comes from birds. Among lekking male sage grouse (*Centrocercus urophasianus*), condition was negatively correlated with increased display effort (Vehrencamp *et al.* 1989). Part of the reduction in body condition in ungulates is due to lower voluntary feed intake (Kay 1979; Miquelle 1990). Feed intake is partly controlled by sexual hormones, and castrated males typically have a lower reduction in voluntary feed intake and may gain weight during the rutting period (Kay 1979; Ryg 1982). In addition to decreased food intake and fighting, several mechanisms may produce the observed age-dependent pattern of weight loss during the rut. In addition to fighting (Clutton-Brock *et al.* 1982; Alvarez 1993; Pélabon *et al.* 1999), roaring activity (McComb 1987), 'driving' and tending of females (Espmark 1964; Lent 1965; Henshaw 1970) by prime-aged males are also particularly strenuous. Furthermore, the analyses indicated that prime-aged males started rutting earlier (figure 1), which was previously reported for red deer on Rum, Scotland (Clutton-Brock *et al.* 1982) as well as in reindeer (*Rangifer tarandus*) (Espmark 1964).

The observed age-related pattern of reproductive effort is thus quite different for male and female ungulates. Whereas first-time breeding females often incur a greater somatic cost of reproduction than second-time breeders (Sand 1998), young males lost virtually no body weight during the rutting season (figure 1*a*). Studies on fallow deer further suggest that early reproduction in males has no effect on subsequent winter survival (McElligott & Hayden 2000). Younger males nevertheless take an active part during the rut (Clutton-Brock *et al.* 1982; Pemberton *et al.* 1992), but typically have a much lower reproductive

success (Squibb 1985; Pemberton *et al.* 1992; Asa 1999; McElligott & Hayden 2000; Preston *et al.* 2001). After primiparity, older females invest more in their offspring postnatally (Clutton-Brock 1984; Green 1990; Ericsson *et al.* 2001) and are better at targeting their effort (Cameron *et al.* 2000). For example, the condition of red deer calves increased with age of their mother (Clutton-Brock 1984) and older bison mothers showed more tolerance towards—and spent more time nursing—their calves than expected based on age differences in size and presumed milk production (Green 1990).

Reproductive effort in male red deer decreased with increasing density (figure 2). This behaviour differs from previously documented patterns for female red deer on Rum, Scotland, where lactating females were reported to have lower fecundity than non-lactating females, a difference that increased with population density (Clutton-Brock *et al.* 1982, 1983). High population density often leads to female-biased adult sex ratios in highly polygynous species, such as red deer, which decrease competition among males during rut (Clutton-Brock *et al.* 1997). When female numbers rose and the sex ratio became progressively female-biased on Rum, Scotland, (i) the proportion of resident males that held harems during the mating season increased; (ii) the mean age of harem-holding males declined (Clutton-Brock *et al.* 1997); and (iii) there was a reduction in frequency of fights among red deer stags (Clutton-Brock *et al.* 1982). Our result is consistent with these behavioural observations. However, results from red deer contrast with those from populations of non-lekking fallow deer, where increased frequency of fighting with increasing density was observed (Alvarez 1993).

The effect of density on weight loss during the rut was found to be weak in young males, but increased considerably with advancing age, also after prime age was reached (figure 2). Although prime-aged males were much heavier before entering rutting season at low than at high density, weight differences were much smaller after the rutting season had ended. By contrast, for very old males (which are lighter; Mysterud *et al.* 2001*c*), the difference in weight at high and low density was marked also after the rutting season (figure 2). High population density is associated with increased mortality of males relative to females (Coulson *et al.* 1997; Clutton-Brock *et al.* 1997). The same reduction in body weight can possibly lead to a higher overwinter mortality at high than at low density— and more so in senescent males since they enter the rut in poorer condition at high density. Even prime-aged males reduced their reproductive effort at high density. Such a conservative reproductive tactic peaked in old males, which did not lose any further weight during rut at high density. These findings suggest that males do not trade survival for reproductive effort. Male red deer therefore probably reduce reproductive effort (somatic costs of reproduction) at high population density due to associated increased risk of mortality. If so, it may be premature to reject the terminal investment hypothesis because investment refers to reproductive effort relative to costs (Evans 1990).

An alternative interpretation of the lower weight of males at high density when sexual selection is weaker is that they do not give the same priority to growth. In any case, this differs from Soay sheep (*Ovis aries*) ewes, which

do not adjust annual reproductive effort to resource availability, despite wide density-dependent changes in reproductive costs (Clutton-Brock *et al.* 1996).

The different evolutionary trajectories of the sexes, which originate from sexual selection (Darwin 1871), have long been known to be profound (Clutton-Brock *et al.* 1982, 1988). The divergent pattern of reproductive effort of males relative to females with increasing population density and advancing age of the individual further emphasizes the contrasting life histories of male and female ungulates.

REFERENCES

Alvarez, F. 1993 Risks of fighting in relation to age and territory holding in fallow deer. *Can. J. Zool.* **71**, 376–383.

Asa, C. S. 1999 Male reproductive success in free-ranging feral horses. *Behav. Ecol. Sociobiol.* **47**, 89–93.

Bobek, B., Perzanowski, K. & Weiner, J. 1990 Energy expenditure for reproduction in male red deer. *J. Mammal.* **71**, 230–232.

Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference: a practical information-theoretic approach.* New York: Springer.

Cameron, E. Z., Linklater, W. L., Stafford, K. J. & Minot, E. O. 2000 Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behav. Ecol. Sociobiol.* **47**, 243–249.

Clutton-Brock, T. H. 1984 Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* **132**, 212–229.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982 *Red deer. Behaviour and ecology of two sexes.* Edinburgh University Press.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1983 The costs of reproduction to red deer hinds. *J. Anim. Ecol.* **52**, 367–383.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1988 Reproductive success in male and female red deer. In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 325–343. The University of Chicago Press.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1989 Fitness costs of gestation and lactation in wild mammals. *Nature* **337**, 260–262.

Clutton-Brock, T. H., Stevenson, I. R., Marrow, P., MacColl, A. D., Houston, A. I. & McNamara, J. 1996 Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *J. Anim. Ecol.* **65**, 675–689.

Clutton-Brock, T. H., Rose, K. E. & Guinness, F. E. 1997 Density-related changes in sexual selection in red deer. *Proc. R. Soc. Lond.* B **264**, 1509–1516. (DOI 10.1098/rspb.1997. 0209.)

Coulson, T. N., Albon, S. D., Guinness, F. E., Pemberton, J. M. & Clutton-Brock, T. H. 1997 Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). *Ecology* **78**, 852–863.

Darwin, C. 1871 *The descent of man, and selection in relation to sex.* New York: Appleton.

Dzieciolowski, R., Babinska-Werka, J., Wasilewski, M. & Goszczynski, J. 1996 Physical condition of red deer in a high density population. *Acta Theriol.* **41**, 93–105.

Ericsson, G., Wallin, K., Ball, J. P. & Broberg, M. 2001 Age-related reproductive effort and senescence in free-ranging moose, *Alces alces. Ecology* **82**, 1613–1620.

Espmark, Y. 1964 Rutting behaviour in reindeer (*Rangifer tarandus* L.). *Anim. Behav.* **12**, 159–163.

Evans, R. M. 1990 The relationship between parental input and investment. *Anim. Behav.* **39**, 797–813.

Festa-Bianchet, M., Apollonio, M., Mari, F. & Rasola, G. 1990 Aggression among lekking male fallow deer (*Dama dama*): territory effects and the relationship with copulatory success. *Ethology* **85**, 236–246.

Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J. T. 1998 Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* **152**, 367–379.

Geist, V. 1986 New evidence of high frequency of antler wounding in cervids. *Can. J. Zool.* **64**, 380–384.

Gosling, L. M., Petrie, M. & Rainy, M. E. 1987 Lekking in topi: a high cost, specialist strategy. *Anim. Behav.* **35**, 616–618.

Green, W. C. H. 1990 Reproductive effort and associated costs in bison (*Bison bison*): do older mothers try harder? *Behav. Ecol.* **1**, 148–160.

Green, W. C. H. & Rothstein, A. 1991 Trade-offs between growth and reproduction in female bison. *Oecologia* **86**, 521–527.

Hamlin, K. L., Pac, D. F., Sime, C. A., DeSimone, R. M. & Dusek, G. L. 2000 Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *J. Wildl. Mngmt* **64**, 441–449.

Hastie, T. & Tibshirani, R. 1990 *Generalized additive models.* London: Chapman & Hall.

Henshaw, J. 1970 Consequences of travel in the rutting behaviour of reindeer and caribou (*Rangifer tarandus*). *Anim. Behav.* **18**, 256–258.

Jönsson, K. I. 1997 Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57–66.

Kay, R. N. B. 1979 Seasonal changes of appetite in deer and sheep. *ARC Res. Rev.* **5**, 13–15.

Kojola, I. 1985 Influence of age on the reproductive effort of male reindeer. *J. Mammal.* **72**, 208–210.

Komers, P. E., Messier, F. & Gates, C. C. 1994 Plasticity of reproductive behaviour in wood bison bulls: on risks and opportunities. *Ethol. Ecol. Evol.* **6**, 485–495.

Lent, P. C. 1965 Rutting behaviour in a barren-ground caribou population. *Anim. Behav.* **13**, 259–264.

McComb, K. 1987 Roaring by red deer stags advances the date of oestrus in hinds. *Nature* **330**, 648–649.

McElligott, A. G. & Hayden, T. J. 2000 Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). *Behav. Ecol. Sociobiol.* **48**, 203–210.

Maher, C. R. & Byers, J. A. 1987 Age-related changes in reproductive effort of male bison. *Behav. Ecol. Sociobiol.* **21**, 91–96.

Miquelle, D. G. 1990 Why don't bull moose eat during the rut? *Behav. Ecol. Sociobiol.* **27**, 145–151.

Mysterud, A., Yoccoz, N. G., Stenseth, N. C. & Langvatn, R. 2000 Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J. Anim. Ecol.* **69**, 959–974.

Mysterud, A., Langvatn, R., Yoccoz, N. G. & Stenseth, N. C. 2001*a* Plant phenology, migration and geographic variation in body weight of a large herbivore: the effect of a variable topography. *J. Anim. Ecol.* **70**, 915–923.

Mysterud, A., Stenseth, N. C., Yoccoz, N. G., Langvatn, R. & Steinheim, G. 2001*b* Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* **410**, 1096–1099.

Mysterud, A., Yoccoz, N. G., Stenseth, N. C. & Langvatn, R. 2001*c* The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent sen-

escence. *Proc. R. Soc. Lond.* B **268**, 911–919. (DOI 10.1098/rspb.2001.1585.

Pélabon, C., Komers, P. E. & Höglund, J. 1999 Do leks limit the frequency of aggressive encounters in fallow deer? Linking local male density and lek occurrence. *Can. J. Zool.* **77**, 667–670.

Pemberton, J. M., Albon, S., Guinness, F. E., Clutton-Brock, T. H. & Dover, G. A. 1992 Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behav. Ecol.* **3**, 66–75.

Pianka, E. R. & Parker, W. S. 1975 Age-specific reproductive tactics. *Am. Nat.* **109**, 453–464.

Preston, B. T., Stevenson, I. R., Pemberton, J. M. & Wilson, K. 2001 Dominant rams lose out by sperm depletion. A waning success in siring counters a ram's high score in competition for ewes. *Nature* **409**, 681–682.

Ryg, M. 1982 Seasonal changes in weight gain, growth hormone, and thyroid hormones in intact and castrated male moose (*Alces alces*). *Can. J. Zool.* **60**, 2941–2946.

Sand, H. 1998 Costs of reproduction in female moose (*Alces alces*) as measured by means of phenotypic correlations. *Can. J. Zool.* **76**, 187–193.

Squibb, R. C. 1985 Mating success of yearling and older bull elk. *J. Wildl. Mngmt* **49**, 744–750.

Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.

Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989 The energetic cost of display in male sage grouse. *Anim. Behav.* **38**, 885–896.

Venables, W. N. & Ripley, B. D. 1994 *Modern applied statistics with S-plus*. New York: Springer.

Williams, G. C. 1966 *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press.

Visit http://www.pubs.royalsoc.ac.uk to see an electronic appendix to this paper.