

Early determinants of lifetime reproductive success differ between the sexes in red deer

L. E. B. Kruuk^{1,2*}, T. H. Clutton-Brock¹, K. E. Rose¹ and F. E. Guinness¹

¹Large Animal Research Group, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

²Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh EH9 3JT, UK

In polygynous, sexually dimorphic species, sexual selection should be stronger in males than in females. Although this prediction extends to the effects of early development on fitness, few studies have documented early determinants of lifetime reproductive success in a natural mammal population. In this paper, we describe factors affecting the reproductive success of male and female red deer (*Cervus elaphus*) on the island of Rum, Scotland. Birthweight was a significant determinant of total lifetime reproductive success in males, with heavier-born males being more successful than lighter ones. In contrast, birthweight did not affect female reproductive success. High population density and cold spring temperatures in the year of birth decreased several components of fitness in females, but did not affect the breeding success of males. The results confirm the prediction that selection on a sexually dimorphic trait should be greater in males than in females, and explain the differential maternal expenditure between sons and daughters observed in red deer. Differences between the sexes in the effects of environmental and phenotypic variation on fitness may generate differences in the amount of heritable genetic variation underlying traits such as birthweight.

Keywords: *Cervus elaphus*; lifetime reproductive success; density dependence; early development; sexual selection

1. INTRODUCTION

In polygynous, sexually dimorphic species, variance in the lifetime reproductive success (LRS) of males far exceeds that in females (Darwin 1871). This generates the testable prediction that differences between individuals should be more important in determining fitness in males than females, and hence that the intensity of sexual selection on particular traits should be stronger in males (Andersson 1994). By corollary, levels of parental investment during early development should also have a greater effect on the fitness of males than females (Trivers & Willard 1973). However, an understanding of patterns of selection in natural populations also requires an understanding of the effect of ecological or environmental factors on fitness (Travis *et al.* 1985). Furthermore, in sexually dimorphic species, because of the associated differences between the sexes in growth patterns and energy expenditure, the effects of ecological factors on fitness should differ between males and females: for example, the effect on adult breeding success of environmental conditions during early development is predicted to differ between the sexes in dimorphic species (Lindström 1999).

Because LRS in both sexes is not easily ascertained in the wild, the above predictions have rarely been tested in a natural mammal population. In this paper, we compare and contrast early determinants of LRS in male and female red deer (*Cervus elaphus*) on the Isle of

Rum, Scotland. In red deer, a female's reproductive success per year is never more than one, whereas a male, who provides no parental care, may father several offspring. The statistical variance in LRS of males is therefore more than three times that of females (Rose *et al.* 1998). Here, we compare the intensity of selection on a sexually dimorphic trait, birthweight, in males and females. We also document changes in total LRS over a period of increasing population density and hence (we assume) of decreasing resource availability, and compare the relative effect of this, and other environmental conditions during early development, on fitness in the two sexes.

Differential effects of environmental conditions and the influence of phenotypic characters on fitness will generate differences in the heritability of a trait, defined as the proportion of its total variance which is genetically determined. In any population, an individual's fitness is determined by its genotype, the environment and any interaction between the two (Falconer & Mackay 1996), as well as a large portion of chance. The potential for evolution is therefore dependent on the relative magnitude of the genetic and environmental factors: if the latter are sufficiently strong, they will confound the opportunity for selection to affect gene frequencies. Conversely, if the environment has little effect on fitness, the efficacy of selection in removing unfit genotypes will be far greater. However, because populations are composed of heterogeneous individuals for whom the relative effects of environment and genotype may vary, single parameter estimates for a whole population may be misleading. In this study,

*Author for correspondence (loeske.kruuk@ed.ac.uk).

we show that the relative effects on fitness of environmental variation and genotype can differ significantly between the two sexes.

The data afford a test for interactions between the effects of phenotypic and environmental variation. It is not clear whether environmental stress should increase or decrease the strength of sexual selection of a particular trait. Geist (1971) has suggested that, in ungulates, as populations approach carrying capacity, males may be unable to expend as much energy on mating competition, with the result that both variation in mating success and the intensity of selection on secondary sexual characters decline. With the increasingly female-biased adult sex ratio observed in the Rum population, competition for mates and hence the opportunity for selection has decreased with increasing density (Clutton-Brock *et al.* 1997). However, studies of the effects of environmental stress on traits in this red deer and other large mammal populations have consistently reported intensified natural selection (Clutton-Brock *et al.* 1987; Festa-Bianchet *et al.* 1998; Milner *et al.* 1999).

The effects of birthweight and population density on breeding success in the red deer from Rum have been described in previous studies (Albon *et al.* 1987; Clutton-Brock *et al.* 1987, 1988; Rose *et al.* 1998). However, a direct comparison of the relative effects of early development on fitness in either sex has not been made, and this is crucial for an understanding of patterns of both sexual selection and maternal investment. We therefore recast earlier analyses using an enlarged data set describing the total LRS of both sexes. Analysis at the individual rather than cohort (as in Albon *et al.* 1987; Clutton-Brock *et al.* 1987; Rose *et al.* 1998) level allows a comparison of within- and between-cohort effects. We consider measures of LRS and four component factors to test the following predictions: (i) that sexual selection on individual phenotypic variation is more important in males than in females; (ii) that the effects of the environmental conditions experienced during early development differ between the sexes; and (iii) that the strength of sexual selection on phenotypic traits intensifies with environmental stress.

2. METHODS

(a) *Study area and population*

Data were collected within an area of *ca.* 12 km² in the north of the Isle of Rum, Inner Hebrides, Scotland, between 1971 and 1997. The red deer (*C. elaphus*) population in this area has not been culled since 1973, since when the number of adult females more than trebled to approximately 160, whilst the number of adult males decreased by almost half to approximately 110. All red deer living in the study area are known individually and are monitored in weekly censuses (for further details, see Clutton-Brock *et al.* 1982).

The analysis considers individuals born up to and including 1984, who had been weighed at birth, who had survived to breeding age (taken to be three years in females and five years in males) and who died a natural death, giving a total of 101 females and 66 males: juvenile mortality in males is greater than in females, and males are more likely to emigrate from the study area. An additional six males aged 12 or more when last seen were also included in the analysis, as more than 95% of LRS has been achieved by this age in males (Marshall 1998).

(b) *Estimating breeding success*

The breeding success of females was determined from censuses, since calves remain with their mothers for at least a year. That of males was estimated using daily observations made during the mating season, during which adult males herd females into harems. A male was assumed to be the father of a calf if its mother was seen to be in oestrous whilst in his harem, or if she was in his harem for longest during an 11-day window around her estimated conception date (Clutton-Brock *et al.* 1997).

(c) *Fitness components*

The following fitness measures were considered. (i) LRS: total number of offspring born to a female or sired by a male which survived to two years old; (ii) offspring survival: proportion of an individual's offspring surviving to two years; (iii) lifetime breeding success (LBS): total number of offspring born to a female or sired by a male; (iv) female fecundity: proportion of years of her breeding life span (from three years old until death) in which a female produced a calf; (v) male maximum annual breeding success (ABS): as male breeding success varies with age, the maximum value in one year was considered instead of an average breeding success; and (vi) longevity: age at death, in years, for all animals.

(d) *Explanatory variables*

The fitness measures were related to: (i) total population density: number of females at least one year old, resident in the study site during an individual's year of birth; (ii) local population density: a measure of the spatial proximity of individuals, calculated using a hierarchical cluster analysis (Coulson *et al.* 1997). As calves stay with their mothers during their first year of life, individuals were assigned their mother's local population density for that year; (iii) birthweight: estimated from the weight (kg) of individuals captured up to 14 days after birth, assuming a gain of 0.015 kg h⁻¹ since birth (Clutton-Brock *et al.* 1982); (iv) weather variables: the total rainfall (mm) and average temperature (°C) during April and May immediately prior to the individual's birth, and the total rainfall from October to January in the individual's year of birth were initially included in all analyses. Spring temperature affects *in utero* growth rates (Albon *et al.* 1987), whereas winter precipitation affects calf survival (Coulson *et al.* 1997).

Sample sizes for each cohort and further details of paternity assignment methods and the variables analysed are given in the electronic appendix to this paper found on the Royal Society Web site.

(e) *Statistical analysis*

Correlation coefficients between fitness components were calculated, with significance levels adjusted using the sequential Bonferroni method (Rice 1989) to correct for multiple comparisons.

The determinants of fitness were analysed using generalized linear models (McCullagh & Nelder 1989). Male LRS, LBS and maximum ABS showed highly skewed distributions, necessitating a negative binomial error structure. Female LRS and LBS were analysed using a Poisson error structure; all negative binomial and Poisson models used a log-link function. Offspring survival and female fecundity were analysed with a binomial error structure, with deviance scaled to remove overdispersion; individuals with no offspring were excluded from this analysis. Longevity fitted a normal distribution, so was analysed using a general linear regression. All analysis was performed in GENSTAT 5, v. 3.2.

Table 1. Correlation coefficients between fitness components in females and males

(* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, after sequential Bonferroni adjustment (Rice 1989).)

sex	component	LRS	offspring survival	LBS	fecundity
females	offspring survival	0.629***	—	—	—
	LBS	0.638***	-0.012	—	—
	fecundity	0.329**	-0.039	0.680***	—
	longevity	0.601***	0.028	0.858***	0.299*
males	offspring survival	0.240	—	—	—
	LBS	0.808***	-0.090	—	—
	maximum ABS	0.660***	-0.062	0.847***	—
	longevity	0.267	-0.049	0.417	0.248

For each fitness measure, a full model containing all explanatory variables and first-order interaction terms was initially fitted. Each term was then dropped from the full model unless doing so had a significant effect on model fit. For models with normal errors, significance was assessed using F ratios. For other error structures, the change in deviance on removal of a term is approximately distributed as χ^2 , with degrees of freedom equal to the change in degrees of freedom for the model.

3. RESULTS

(a) Covariation between fitness components

In females, LRS was significantly positively correlated with all components of fitness considered (table 1). In males, LRS was significantly positively correlated with LBS and maximum ABS but not with longevity or offspring survival (see table 1).

(b) Environmental variation

The generalized linear models for each fitness component are summarized in table 2. The LRS of females declined as the total density in the study area increased (table 2a), due at least partially to a negative effect on fecundity (table 2g).

The local population density experienced by a female in the first year of her life did not affect LRS (table 2a), despite being negatively associated with the survival of her offspring (table 2b). This is presumably because females are philopatric: the local density in a female's first year of life will be correlated with that experienced by her calves, and calf survival is reduced at high local densities (Coulson *et al.* 1997).

With the exception of the survival of their offspring, none of the male fitness measures were affected by total or local population density. Figure 1a,b compares the effects of total population density on male and female LBS.

Spring temperature in a female's year of birth affected her LRS and all component factors (figure 1c). Spring temperature is known to affect the mean birthweight in a year (Albon *et al.* 1987), but here its effects on female fitness were independent of whether or not birthweight was also included in the model (with birthweight: $\chi^2_{(1)} = 7.183$, $p = 0.007$; without, $\chi^2_{(1)} = 8.51$, $p = 0.004$). In contrast, spring temperature had no effect on male fitness measures, again regardless of whether or not birthweight was included in the model (with birthweight, $\chi^2_{(1)} = 0.049$, $p = 0.825$; without, $\chi^2_{(1)} = 0.666$, $p = 0.414$);

see figure 1d. Neither spring rainfall nor winter rainfall had any effect, nor was there any evidence that interactions between any density and weather measures affected fitness in either sex.

(c) Phenotypic variation

Birthweight did not have significant explanatory power in any of the models of female fitness measures (table 2), regardless of whether or not spring temperature was also included (e.g. for LRS, with spring temperature, $\chi^2_{(1)} = 0.981$, $p = 0.322$; without, $\chi^2_{(1)} = 2.31$, $p = 0.129$).

In contrast, birthweight explained a significant proportion of the deviance in male LRS, LBS, calf survival and maximum mating success (table 2). Again, these effects were independent of whether spring temperature was already included in the model (e.g. for LRS, with spring temperature, $\chi^2_{(1)} = 10.62$, $p = 0.001$; without, $\chi^2_{(1)} = 1.24$, $p = 0.001$). Figure 1e,f compares the effects of birthweight on male and female LBS. The outlier in the male sample, with a birthweight of nearly 11 kg and zero breeding success was also never assigned paternities from genetic data, despite being a successful harem holder, so may be infertile.

There were no significant interactions between any of the main effects investigated. In particular, there was no evidence of any interaction between the effects of birthweight and population size on any of the fitness measures, nor between birthweight and spring temperature.

4. DISCUSSION

Our results show marked differences in the factors determining fitness in adult male and female red deer. Birthweight explained a significant proportion of the variation in reproductive success in males, but not in females, supporting the prediction that the intensity of selection on a sexually dimorphic trait should be stronger in males than in females. In contrast, a female's LRS was significantly affected by density and spring temperature in her year of birth, but a male's was not. The coefficients in the regression models afford a direct comparison of the effects on fitness: for LBS, the magnitude of the coefficients for total density, spring temperature and birthweight all differed significantly between the sexes (table 2).

Density (either local or total) affected both offspring survival and female fecundity. Density dependence in juvenile survival is frequently observed in large herbivore populations, but there is less evidence for density

Table 2. *Generalized linear models of fitness components*

(Changes in deviance when each term was dropped from the full model (or F ratio for normal error distributions for longevity). Degrees of freedom (d.f.) = 1 for all χ^2 terms, except residual deviance for which d.f. are given; = (1, residual d.f.) for all F ratios. Significant p -values are given in bold. s.s. = sums of squares.)

term	(a) female LRS			(b) male LRS		
	χ^2	estimates (s.e.)	p	χ^2	estimates (s.e.)	p
total density	4.478	-0.00385 (0.00136)	0.034	0.3204	-0.00267 (0.00596)	0.571
local density	2.671	-0.00607 (0.00386)	0.102	0.1038	-0.0041 (0.0125)	0.747
spring temperature	7.183	0.2394 (0.0904)	0.007	0.0490	-0.093 (0.229)	0.825
birthweight	0.981	0.0601 (0.0605)	0.322	10.6243	0.438 (0.136)	0.001
residual deviance	156.562 (d.f. = 96)			60.87 (d.f. = 67)		
term	(c) females' offspring survival			(d) males' offspring survival		
	χ^2	estimates (s.e.)	p	χ^2	estimates (s.e.)	p
total density	0.022	0.00053 (0.00369)	0.882	6.797	-0.01241 (0.0049)	0.009
local density	7.077	-0.02014 (0.00845)	0.008	2.814	-0.0174 (0.0104)	0.093
spring temperature	0.000	-0.001 (0.149)	1.000	0.266	-0.046 (0.178)	0.606
birthweight	0.615	0.085 (0.108)	0.433	4.192	0.217 (0.114)	0.041
residual deviance	111.835 (d.f. = 94)			60.480 (d.f. = 52)		
term	(e) female LBS			(f) male LBS		
	χ^2	estimates (s.e.)	p	χ^2	estimates (s.e.)	p
total density	5.571	-0.00341 (0.00136)	0.018	0.229	0.00274 (0.00464)	0.632
local density	1.572	0.00388 (0.00309)	0.210	0.489	0.0058 (0.0117)	0.484
spring temperature	13.088	0.2037 (0.0574)	0.000	0.127	-0.053 (0.123)	0.722
birthweight	0.384	0.0303 (0.0397)	0.535	5.572	0.272 (0.128)	0.018
residual deviance	161.779 (d.f. = 96)			78.258 (d.f. = 67)		
term	(g) female fecundity			(h) male maximum ABS		
	χ^2	estimates (s.e.)	p	χ^2	estimates (s.e.)	p
total density	4.97	-0.00488 (0.00220)	0.026	0.134	0.00506 (0.00484)	0.714
local density	0.704	0.00428 (0.00511)	0.401	1.520	0.00361 (0.00983)	0.218
spring temperature	4.88	0.2067 (0.0982)	0.027	0.551	-0.067 (0.178)	0.458
birthweight	0.83	0.0655 (0.0659)	0.362	5.642	0.233 (0.107)	0.018
residual deviance	115.412 (d.f. = 96)			72.728 (d.f. = 67)		
term	(i) female longevity			(j) male longevity		
	F ratio	estimates (s.e.)	p	F ratio	estimates (s.e.)	p
total density	2.21	-0.0197 (0.0127)	0.140	3.05	0.01719 (0.00893)	0.086
local density	0.97	0.0260 (0.0265)	0.328	0.71	-0.0158 (0.0188)	0.403
spring temperature	10.75	1.371 (0.477)	0.001	0.07	0.058 (0.346)	0.792
birthweight	0.09	0.132 (0.348)	0.769	0.03	-0.118 (0.205)	0.863
residual mean s.s.	13.83 (d.f. = 96)			3.735 (d.f. = 61)		

dependence in female fecundity (Gaillard *et al.* 1998). Nevertheless, data from two sheep species (*Ovis aries* and *Ovis canadensis*) suggest that even in highly fecund species the costs of reproduction become evident at high densities, leading to a decrease in fecundity (Clutton-Brock *et al.* 1996; Festa-Bianchet & Jorgenson 1998). In the red deer from Rum, the effect of density on female breeding success was presumably mediated through detrimental effects on adult condition.

In contrast, male mating success was not reduced by density. As density rose, mortality among juvenile males increased at a greater rate than among females, resulting in a shift from an artificially maintained male-biased adult sex ratio to a heavily female-biased one, and hence in reduced competition between males for mates (Clutton-Brock *et al.* 1997). The effects of increasing environmental stress are therefore confounded with those of changing population structure, in particular changing

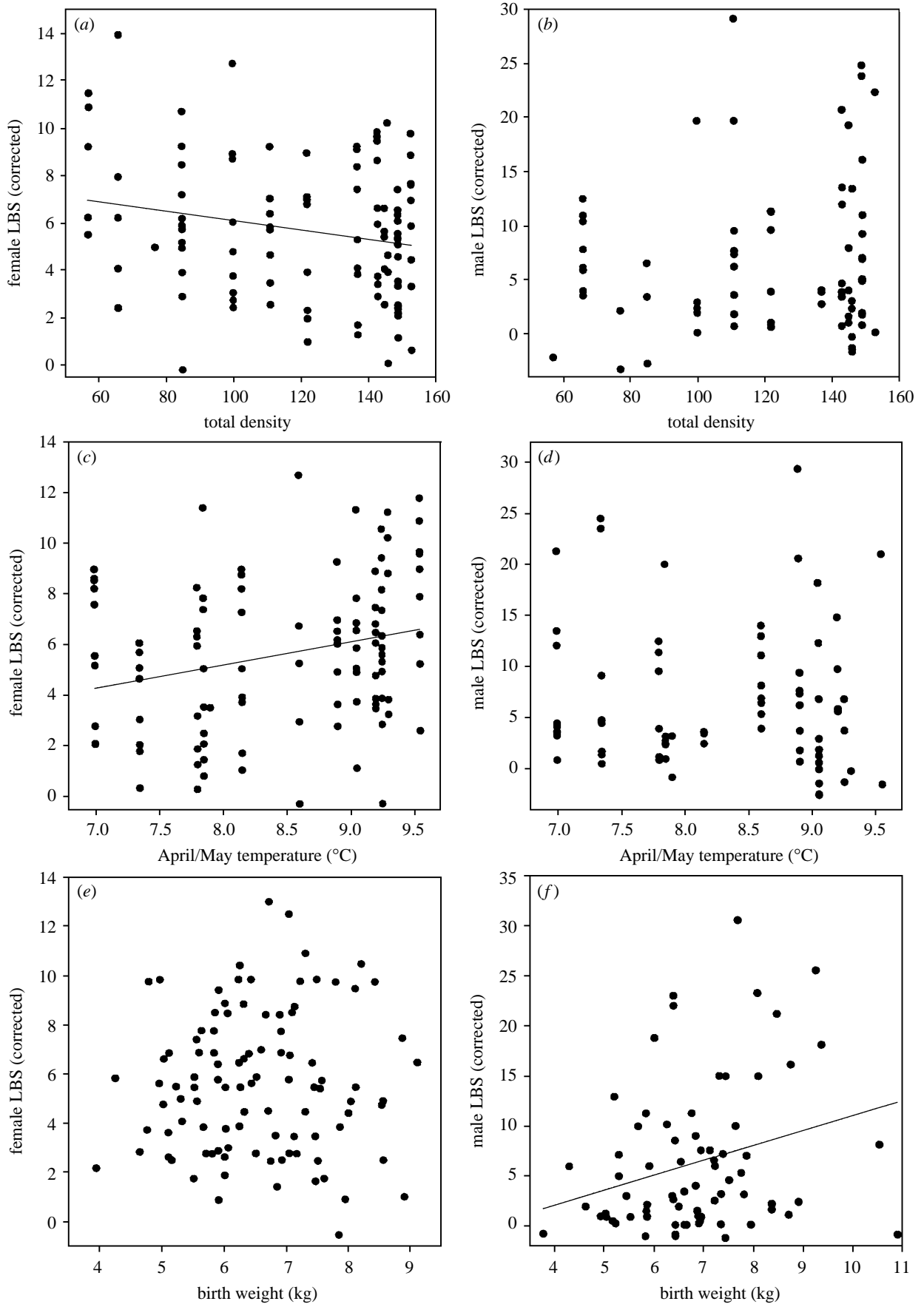


Figure 1. LBS plotted against (a, b) total population density in year of birth; (c, d) spring temperature in year of birth; (e, f) birthweight for females and males. For each variable, LBS values shown are corrected for possible effects of other variables (e.g. values for total population density are corrected for effects of spring temperature, local density and birthweight); regression line from the generalized linear model is given where the relationship is significant.

operational sex ratio (Emlen & Oring 1977). However, note that the density measure considered here was that experienced in the year of birth, which, for a long-lived animal in a growing population, will be different from that experienced at prime breeding age: at least some of the observed difference between the sexes must be due to a different legacy of the density experienced during early development. In contrast, in Soay sheep (*O. aries*), where juvenile survival is also density dependent but males breed in their first year of life, density in the year of birth has a strong effect on male breeding success through its effect on first year survival (Coltman *et al.* 1999). Here, we found no evidence of any interaction between the selection pressure on birthweight and the increasing population density, but whether selection on secondary sexual characters such as antlers is affected by density remains to be determined.

A clearer contrast lay in the different effects of spring temperature and birthweight on fitness: spring temperature affected females' breeding success, whereas birthweight affected that of males. In both sexes, the effects were independent of each other, with none of the relationships being affected by the presence of the other variable in the model. A comparable result was observed for mean fecundity in cohorts of three-year-old females, which was associated with spring temperature in the year of birth but not with mean birthweight (Albon *et al.* 1987). These facts are surprising, as the birthweight of calves was positively correlated with spring temperature that year (males: $r=0.40$, $n=72$; females: $r=0.24$, $n=101$ for this sample; see also Albon *et al.* 1987). Here, however, spring temperature must be influencing female calves' fitness in ways other than through direct effects on foetal size; we assume it acts either through effects on maternal condition during lactation or on food availability for the growing calves. Supporting the first suggestion, Coulson *et al.* (1999) showed that the survival of female calves in their first winter was dependent on maternal condition, whereas that of males was associated with their birthweight. Furthermore, in Norwegian red deer both fecundity at two years and adult body weight in females are linked to winter weather whilst females were *in utero*: warm wet winters increased cohort fecundity, but decreased adult body weight, again suggesting that female breeding success is not associated with body size (Post & Stenseth 1999).

Among those reaching breeding age, heavier-born stags had greater LRS than lighter-born stags. Taken in conjunction with the different effects of birthweight on juvenile survival (Coulson *et al.* 1999), the effects of maternal expenditure on offspring fitness clearly differ between the sexes: resources allocated to male foetuses offer a greater marginal return in terms of parental fitness. This prompts the prediction that females should invest more heavily in male offspring (Trivers & Willard 1973), which is indeed the case: male calves are born heavier than females (Clutton-Brock *et al.* 1982). Furthermore, stronger selection for intra-uterine growth in male embryos may increase their vulnerability to environmental stress (Clutton-Brock 1991), in accordance with the observation of a reduction in the proportion of males born after wet winters and when population density is high (Albon *et al.* 1998; Kruuk *et al.* 1999). Our results on

spring temperature and birthweight suggest that the pressures of sexual selection impel males to obtain maximum maternal resources, aiming to maximize growth rates despite the increased risk of starvation; in contrast, female calves may be more ready to minimize such risks by adjusting their demands, and hence their growth rates, according to the available resources and prevailing environmental conditions (Clutton-Brock 1991).

There is an anomaly between these results and those of Rose *et al.* (1998), who found a significant positive correlation between the mean male LBS of a cohort and the spring rainfall in the year of birth; in contrast, we found no effect of spring rainfall on individual adult breeding success in either sex. The difference may be due to the fact that Rose *et al.* considered males surviving to two years of age, whereas here we considered males surviving to five years, as paternities are almost never attributed to individuals of four years or younger (Marshall 1998). For the years considered here (1971–1985), there was a positive correlation ($r=0.593$, $n=15$) between the proportion of individuals reaching five years of age and the spring rainfall in their year of birth: if spring rainfall affects survival to five years, it may have affected the values of cohort mean breeding success used by Rose *et al.*

Female LRS was thus more strongly influenced by environmental conditions in the year of birth than was that of males, whereas between-individual phenotypic differences at birth were more important in males. Such contrasting determinants of fitness in different groups highlight the need to understand a population's ecology before attempting to estimate the effect of genotype on fitness (e.g. Travis *et al.* 1985). In this case, given the differing influence of birthweight on breeding success in the two sexes, the pressure of sexual selection would be expected to erode genetic variation for birthweight more in males than in females (Fisher 1930). Single estimates for heritability values or variance component estimates averaged across heterogeneous groups may be at best approximate and at worse misleading in their representation of the relative importance of genetic and environmental variation.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

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