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# Cohort variation in male survival and lifetime breeding success in red deer

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## Summary

1. We investigated cohort differences in the lifetime breeding success and survival of male red deer *Cervus elaphus* L. in an increasing population on the Isle of Rum, Scotland.

2. There were significant differences in survival through different stages of the life span between 15 cohorts of males, ranging between: 0.26–1.00, calf survival through first winter; 0.56–1.00, yearling survival; 0.44–0.94, adult survival. This variation in survival was related to environmental conditions in the cohorts' year of birth, whilst controlling for annual effects.

3. For 10 cohorts of males with complete lifetime data, mean breeding success also varied significantly, between 0.83 and 3.86. This variation, too, was associated with environmental conditions in the cohorts' year of birth.

4. Since in many sexually dimorphic mammals, the growth and survival of males is more strongly affected by adverse environmental conditions than that of females, we expected that cohort variation would be more extreme amongst males than females. This was true, for both cohort survival and reproduction.

5. We expected to observe selection on cohort adult body size, related to survival or reproduction. However, there was no evidence of variation in adult body size between cohorts, nor for relationships between differences in body size between cohorts and measures of survival or breeding success. Cohorts which underwent high initial mortality subsequently experienced higher adult survival than cohorts not subjected to high density-related selection early in life.

*Key-words:* body size, demography, density-dependent, density-independent, sexual selection.

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## Introduction

Studies from a wide range of species have shown that female survival and breeding success may be strongly influenced by variation in early development (e.g. *Drosophila*: Partridge 1988; *Parus major*: McCleery & Perrins 1988; van Noordwijk & van Balen 1988; *Brantus bernicla*: Sedinger & Flint 1995; *Cervus elaphus*: Guinness, Albon & Clutton-Brock 1978a; Guinness, Clutton-Brock & Albon 1978b; Clutton-Brock *et al.* 1987; *Homo sapiens*: Borgerhoff Mulder 1988). In long-lived species, these effects can generate substantial differences in survival and breeding success between successive cohorts which may persist throughout the cohort's life span (Albon, Clutton-

Brock & Guinness 1987; Albon, Clutton-Brock & Langvatn 1992).

Several studies have explored the extent of cohort variation amongst females (Albon *et al.* 1987) and demonstrated their considerable demographic consequences (Albon & Clutton-Brock 1988; Albon *et al.* 1992). However, no studies so far have documented cohort effects in males. In many polygynous, sexually dimorphic mammals, the growth and survival of males is more strongly affected by adverse environmental conditions than that of females (Glucksman 1974; Clutton-Brock, Albon & Guinness 1982; Stevenson 1994) and cohort variation in male survival and reproduction might consequently be expected to be more pronounced than in females. When early conditions produce variation in adult body size, we might also observe a significant relationship between mean body size, survival and reproduction for entire cohorts of males. For example, juvenile survival is closely related

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to individual birth weight in male red deer (Rose 1995), and we might consequently expect heavy-born cohorts to show higher juvenile survival. Similarly, there is evidence for direct sexual selection for increased male body size in our population, resulting from the increased duration of harem holding and breeding success of larger males (Rose 1995). Thus, body size variation between cohorts could have implications for sexual selection and for the breeding success of entire cohorts of males.

In cohorts of growing individuals, it is assumed that the increase in total cohort weight associated with individual growth will eventually cease, because of structural constraints or resource limitations. Thus, the total weight of the cohort will approach a constant, giving an inverse relationship between mean cohort weight and density over time (Westoby 1984). This reduction in density accompanying and interacting with the increasing size of individuals in a cohort or population is referred to as density-dependent selection, or 'self-thinning' (Yoda *et al.* 1963; Harper 1977). Density is predicted to be related to weight with a  $-1.33$  gradient in animal populations subject to density-dependent selection, because of the scaling of metabolic rate with (mean weight)<sup>0.75</sup> (Begon, Firbank & Wall 1986). However, the concept of density-dependent selection in animal populations remains contentious, and empirical data are limited (but see Begon *et al.* 1986; Elliott 1993; Elliott 1996; Armstrong 1997). We examine the evidence for density-dependent selection in our population and consider its implications for patterns of survival.

The present study describes significant cohort variation in male survival and breeding success in a 25 year study of red deer (*Cervus elaphus* L.) on the Isle of Rum (Inner Hebrides, Scotland). Our analysis focuses on four main questions: (i) Do cohorts show significant variation in rates of juvenile and adult survival, and to which environmental factors is this variation related? (ii) Do cohorts show significant variation in measures of body size known to be under direct selection, and is this variation related to differences in survival between cohorts? Is the density-weight relationship consistent with density-dependent selection (self-thinning)? (iii) Do cohorts show significant variation in mean breeding success? To which factors (including body size) is this variation related? (iv) Is cohort variation in survival and breeding success greater amongst males than in females? For an analysis of this kind, red deer have the advantage that observational estimates of male breeding success (including harem size, duration of harem holding and number of copulations) are consistently correlated with genetic estimates of the number of calves fathered by different males (Pemberton *et al.* 1992).

## Methods

All data used in this analysis were collected in the North Block of Rum (Inner Hebrides, Scotland)

between 1971 and 1990 (Clutton-Brock *et al.* 1982). Since 1972, all the deer living in the North Block have been individually recognized, either by natural variation or artificial marks (Clutton-Brock *et al.* 1982). Between 1971 and 1990, the study population has consisted of 100–150 females and about 60 males of breeding age (Clutton-Brock *et al.* unpublished data). The survival of all individuals in the study population is monitored in five censuses carried out each month (Clutton-Brock *et al.* 1982).

## SAMPLES

The breeding success of all males in the study area is estimated during the annual rut (October–November). Over this period, adult males herd females into harems that they then defend by means of roaring contests and fights (Clutton-Brock *et al.* 1979). A female may be in the harem of a succession of different males in the course of the rut. Due to the size of our study area, the relatively few daylight hours in autumn, and the short duration of overt oestrous (females are receptive for only a few hours), we rarely observe more than 10% of females being mated. However, from all-day focal watches, it is clear that matings are normally between a harem-holder and a harem female, that it is rare for a female to mate more than once per oestrous, and extremely unusual for a female to mate with more than one male. Through a daily census (by FEG), we collect virtually complete data on which male's harem each female is in (if any) on each day of the rut, as well as opportunistic data on mating and other behaviour associated with oestrous, e.g. mounting and chivying (Clutton-Brock *et al.* 1982).

Estimates of individual breeding success were based on observations of the rutting behaviour of 166 males that were born in the study area between 1971 and 1980 and which survived to 2 years old. The conception date of each calf born throughout the study period was estimated by subtracting the population mean gestation length (235 days, Guinness *et al.* 1978a) from the calf date of birth. A male was identified as the potential father of a calf if the mother was in his harem during the 11-day period on and around the conception date ( $\pm 1$  standard deviation of the gestation period). For each day that a male held a female which subsequently gave birth, he was awarded 1/11 of the paternity of the calf. For each male, these fractions were summed over the entire life span to calculate lifetime breeding success (Clutton-Brock *et al.* 1982).

For all males born in a given year for which data were available, we calculated the cohort mean value for the following measures.

*Birth date:* individual calf birth date was the number of days after 1 May in the year of birth (Clutton-Brock *et al.* 1982).

*Birth weight:* was estimated for calves captured up

to 14 days after birth. Individual birth weight (kg) was estimated by subtracting 0.36 kg from the capture weight for each day between birth and capture (Guinness *et al.* 1978a).

*Adult body size:* three measures of adult size, known to be related to individual breeding success (Clutton-Brock *et al.* 1988) and demonstrated to be under direct sexual selection (Rose 1995), were included: Hind foot length was the distance (cm) from the point of the hock to the posterior edge of contact between the hoof and the ground (Suttie & Mitchell 1983); Jaw length was the distance (mm) from the outer point of the fourth incisor socket to the posterior edge (Suttie & Mitchell 1983); The third measure was body weight (kg). To control for age effects on size, individual jaw length was the residual from an exponential relationship between jaw length and age at measurement, and cohort jaw length was the mean of the residual values for cohort members. Similarly, age effects on individual hind foot length and body weight were controlled for using linear models and calculating mean cohort values from the residuals.

*Cohort survival.* Summer calf survival (0–4 months): the proportion of the cohort that survived from birth till 1 October in the year of birth; Winter calf survival (5–12 months): the proportion of the cohort alive on 1 October that survived till 30 April the following year; Yearling survival (13–24 months): the proportion of the cohort alive on 30 April that survived till 1 May the following year (Clutton-Brock *et al.* 1982); Adult survival (2–8 years): the proportion of the cohort alive on their second birthday that survived till 8 years old. Survival through each of the above stages was calculated for both male and female cohort members.

*Lifetime breeding success.* For males, individual lifetime breeding success was estimated using the method described above. Female breeding success was calculated as the total number of offspring produced that survived beyond their second birthday. For each sex, the mean and variance of lifetime breeding success were calculated across all individuals from each cohort that survived to at least 2 years of age.

The following environmental variables were also included.

*Female population density:* the number of adult ( $\geq 2$  years old) females resident in the study area. This was used in preference to the combined number of males and females in the study population, since previous analyses (Clutton-Brock, Major & Guinness 1985) have shown reproduction and survival to be related to female density more closely than combined density. Individuals were defined as resident if they were seen in at least 10% of censuses in any 4-month period (Clutton-Brock *et al.* 1982).

*Temperature:* the mean temperature ( $^{\circ}\text{C}$ ) in April and May of a cohort's year of birth. The birth weight and survival of cohorts of females and their offspring is related to temperature in these months, the last 2

months of gestation (Albon, Clutton-Brock & Guinness 1983; Albon *et al.* 1987).

*Rainfall:* the total precipitation (mm) during April and May in a cohort's year of birth. Previous analyses (Albon & Clutton-Brock 1988; Rose 1995) suggest that reproductive performance and juvenile survival are related to rainfall in the last 2 months of gestation.

#### STATISTICAL ANALYSIS

Our analysis focused principally on members of 10 cohorts born between 1971 and 1980, all of whose members had died by 1993. However, sample sizes vary for different measures (see Table 1). For example, while there were complete data on breeding success for 10 cohorts, there were data on survival to 2 years for 21 cohorts that had passed through the juvenile mortality stage. Consequently, residual degrees of freedom vary throughout the analysis. Numbers of males born into each cohort are shown in Table 1, for numbers of females born see Albon *et al.* (1987).

Genstat Version 5.3 (Genstat 5 Committee 1993) was used for parametric tests and Statview Version 4.0 for non-parametric tests. Significant cohort variation in body size and breeding success, both continuous variables, was tested for by fitting year of birth to individuals' values in linear regression analyses. Significance was tested using *F* ratios (Sokal & Rohlf 1981). Cohort survival was measured as a mean probability and significant variation was tested for using *G*-tests (Seigel & Castellan 1988). Associations between cohort survival and environmental conditions in the year of birth were tested using Spearman Rank Order correlation coefficients (Seigel & Castellan 1988). Sources of variation in body size and breeding success were investigated using multiple linear regression models. Initially, the 'maximal' model was fitted to the data: this included all the measures to be considered as explanatory variables. Each explanatory variable was then dropped from the maximal model, unless this significantly reduced the variance explained by the model (tested using *F* ratios). Once no more variables could be dropped without reducing the variance explained, variables which were previously dropped were re-instated to confirm their non-significance: the most parsimonious but significant model is the 'minimum' model (Crawley 1994).

Because of the increased risk of making Type II errors when presenting large number multiple comparison tests (Rice 1989), adjusted significance levels were calculated by applying a sequential Bonferroni method at the table-wide level. Thus, for each statistic we present two significance levels: one for the test criterion  $P < 0.05$  and one for  $P_i \leq [1 - (1 - \alpha)^{1/(1+k-1)}]$ . For the sake of brevity, adjusted statistics which are significant are marked BS (Bonferroni significant), and those which are not significant are marked BNS (Bonferroni non-significant).

**Table 1.** Survival rates of males born into different cohorts since 1971. Juvenile survival is measured over the first 2 years of life and is also subdivided into summer and winter calf survival, and yearling survival. Adult survival is calculated as an annual rate, from 2 to 8 years. For some measures, the data were incomplete, since some cohorts had not reached the relevant stage of the life span: these years are marked with ‘–’

Cohort	Number of males born	Mean cohort birth date (days after 1 May)	Mean cohort birth weight (kg)	Summer calf survival 0–4 months	Winter calf survival 5–12 months	Yearling survival 13–24 months	Total juvenile survival 0–2 years	Annual adult survival rate 2–8 years
1972	15	33.69	6.41	0.93	0.93	1.00	0.87	0.54
1973	25	36.75	6.25	0.96	1.00	1.00	0.96	0.79
1974	17	35.42	7.07	0.88	0.93	0.93	0.76	0.69
1975	27	39.12	7.45	0.78	0.76	0.88	0.52	0.64
1976	26	33.85	6.30	0.88	0.78	1.00	0.69	0.44
1977	32	45.00	7.31	0.81	0.92	0.88	0.66	0.62
1978	38	39.97	6.42	0.92	0.91	0.69	0.58	0.82
1979	32	42.39	6.63	0.78	0.68	0.88	0.47	0.87
1979	37	39.89	5.98	0.86	0.72	0.74	0.46	0.82
1980	31	50.30	6.85	0.77	0.63	0.60	0.29	0.89
1981	37	45.25	7.28	0.92	0.62	0.81	0.46	0.94
1982	42	39.79	6.41	0.81	0.38	0.92	0.29	0.75
1983	39	39.89	6.21	0.85	0.85	1.00	0.72	0.86
1984	43	46.29	6.68	0.86	0.92	0.62	0.49	0.76
1985	51	43.44	6.45	0.94	0.48	1.00	0.45	0.87
1986	25	44.86	6.89	0.88	0.77	0.94	0.56	–
1987	39	44.70	6.21	0.90	0.77	0.56	0.38	–
1988	29	41.72	7.08	0.86	0.36	1.00	0.31	–
1989	33	43.53	6.84	0.85	0.86	0.96	0.70	–
1990	44	34.77	7.35	0.86	0.63	1.00	0.55	–
1991	43	36.31	6.58	0.81	0.46	0.69	0.36	–
1992	41	37.46	6.68	0.85	0.26	–	–	–
1993	22	43.38	7.10	0.91	–	–	–	–

## Results

### VARIATION IN COHORT SURVIVAL

Although there were no significant differences between cohorts in calf survival through the first summer (which ranged from 0.77 to 0.96;  $G = 34.61$ ,  $P > 0.05$ , BNS,  $n = 23$ ), there were significant differences in survival between cohorts of males through all other stages of the life span (Table 1): survival through the first winter: 0.26–1.00 ( $G = 100.77$ ,  $P < 0.001$ , BS,  $n = 22$  years); survival through the second year: 0.56–1.00 ( $G = 42.48$ ,  $P < 0.01$ , BS,  $n = 21$  years); survival from 2 to 8 years: 0.44–0.94 ( $G = 26.22$ ,  $P < 0.05$ , BS,  $n = 15$  years).

These differences in survival were related to environmental factors in the cohorts' year of birth. Survival of calves through their first winter declined as the number of females in the study population increased ( $r_s = -0.681$ ,  $P = 0.002$ , BS,  $n = 22$ , Fig. 1a). Survival of yearlings was not related to female population size ( $r_s = -0.131$ ,  $P = 0.559$ , BNS,  $n = 21$ ) but decreased with the cohort's birth date ( $r_s = -0.527$ ,  $P = 0.016$ , BS,  $n = 21$ , Fig. 1b), with late-born cohorts showing higher mortality.

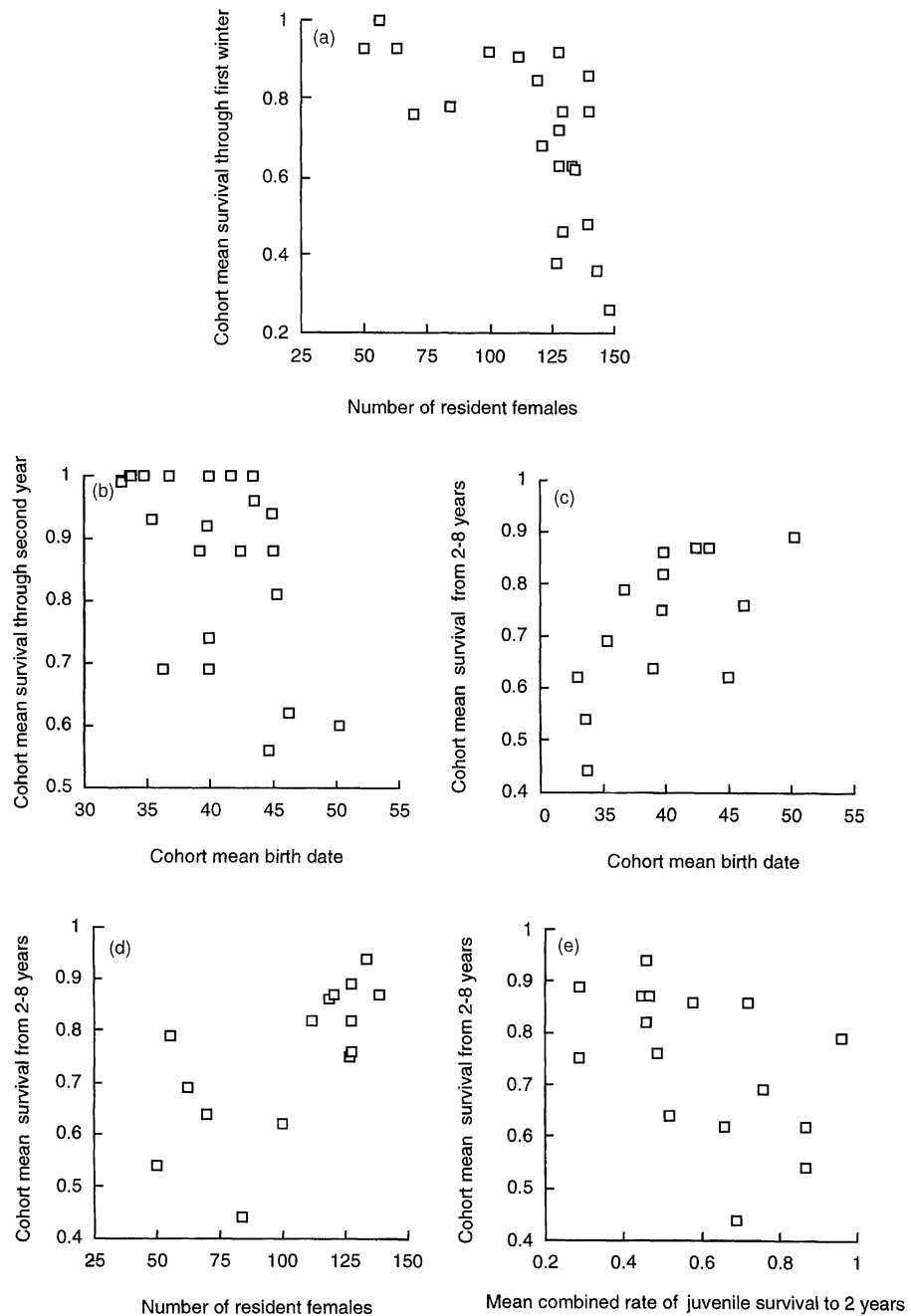
Cohorts which experienced low survival to 24 months were subsequently more likely to survive between

the ages of 2 and 8 ( $r_s = -0.589$ ,  $P = 0.023$ , BS,  $n = 16$ , Fig. 1e). In contrast to juvenile survival, adult survival increased in late-born cohorts and was positively correlated with mean birth date ( $r_s = 0.705$ ,  $P = 0.006$ , BS,  $n = 16$ , Fig. 1c). In addition, male adult survival increased with female population density ( $r_s = 0.729$ ,  $P = 0.006$ , BS,  $n = 15$ , Fig. 1d).

### BODY SIZE AND SURVIVAL

We initially expected that, within cohorts, the birth weight of males that survived to 2 years would be significantly heavier than that of males that died before reaching two. However, in all cohorts that had passed through the juvenile mortality phase, we observed no such difference ( $F_{1,38} = 1.42$ ,  $P = 0.241$ , one-way ANOVA).

For members of the 1971–80 cohorts, there were no significant differences between cohorts in the three measures of adult body size examined, after controlling for individual age at measurement: mean jaw length ( $F_{9,61} = 0.56$ ,  $P = 0.825$ ); mean hind foot length ( $F_{8,36} = 1.36$ ,  $P = 0.249$ ); mean body weight ( $F_{8,37} = 1.11$ ,  $P = 0.382$ ). Nor were there any associations between mortality and adult body size, after calculating the adjusted test criteria (Table 2).



**Fig. 1.** Cohort mean rates of male survival through different stages of the life span, in relation to conditions in the cohorts' year of birth. Sample sizes for each survival stage vary between cohorts in relation to the number of cohorts that have reached a particular age. (a) Winter calf survival from 5 to 12 months, plotted against the number of adult females resident in the study area. (b) Yearling survival from 13 to 24 months, plotted against the cohorts' mean birth date. (c) Adult survival from 2 to 8 years, plotted against the cohorts' mean birth date. (d) Adult survival from 2 to 8 years, plotted against the number of adult females resident in the study area. (e) Adult survival from 2 to 8 years, in relation to combined cohort survival from 0 to 2 years.

**Table 2.** Spearman rank correlations for the relationship between cohort mean adult body size and survival through different stages of the lifespan, for cohorts of males born between 1971 and 90. Significance at  $P < 0.05$  indicated by \*\*. However, no correlations were significant after calculating the table-wide Bonferroni test criteria (see Methods)

	0-4 months	5-12 months	13-24 months	0-2 years	2-8 years
Jaw length (mm)	-0.223	-0.470**	0.041	-0.317	0.227
Hind foot length (cm)	0.261	0.090	-0.036	0.169	-0.029
Body weight (kg)	0.031	-0.049	-0.219	-0.112	0.007

For those cohorts where two or more individuals were weighed both as neonates and as adults (1974–79), we tested for density-dependent selection within each cohort by calculating the gradient of the relationship through time between individual weight and density of cohort members surviving at the time of weighing. This relationship is predicted to approximate  $-1.33$  following density-dependent selection (Begon *et al.* 1986). For each cohort examined, the gradient ( $b$ ) was negative, confirming the action of density-dependent selection at some stage of the life span. However, the gradient also differed significantly from  $-1.33$  in all years except 1978 (1974:  $b = -2.518$ ,  $t = -4.50$ ,  $P < 0.001$  1975:  $b = -2.162$ ,  $t = -6.17$ ,  $P < 0.001$  1976:  $b = -2.439$ ,  $t = -11.27$ ,  $P < 0.001$  1977:  $b = -2.173$ ,  $t = -5.25$ ,  $P < 0.001$  1978:  $b = -1.46$ ,  $t = -0.85$ ,  $P > 0.41979$ :  $b = -2.25$ ,  $t = -6.22$ ,  $P < 0.001$ ; Fig. 2).

#### BREEDING SUCCESS

For the 10 cohorts with complete data, mean lifetime breeding success varied significantly between cohorts from 0.83 to 3.86 calves fathered ( $F_{9,155} = 4.84$ ,  $P < 0.001$ ).

The breeding success of different cohorts was positively correlated with environmental conditions in the first year of life: the mean breeding success of cohorts increased in relation to total rainfall in April and May of the cohorts' year of birth ( $F_{1,8} = 7.14$ ,  $P = 0.028$ , Fig. 3a). After controlling for the effects of rainfall, there was no significant association with mean spring temperature ( $F_{1,7} = 0.14$ ,  $P = 0.75$ ) or female population size ( $F_{1,7} = 0.23$ ,  $P = 0.643$ ) in the cohorts' year of birth.

We found no relationship between cohort body size and breeding success: the mean birth weight of cohort

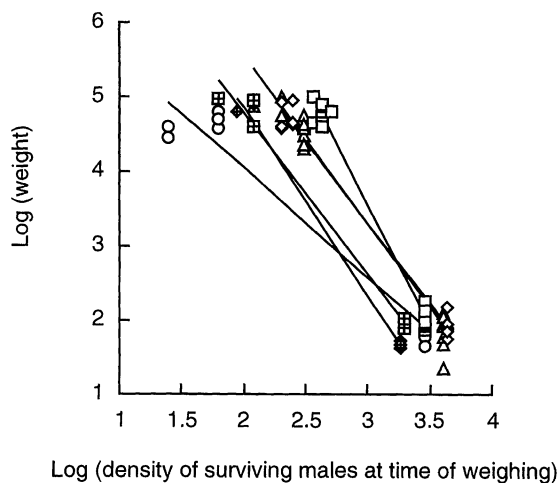


Fig. 2. The relationship between weight (kg) and density of males alive at time of weighing, for six cohorts of males: 1974 (○) 1975 (□) 1976 (△) 1977 (◇) 1978 (○) 1979 (△). Data for each year cover two time periods: weight at birth (lower right) and weight as adult (upper right).

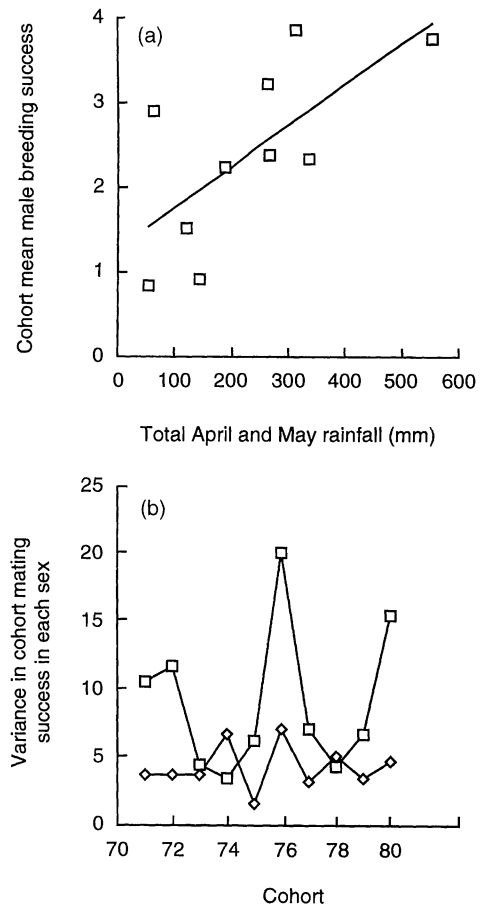


Fig. 3. Variation in breeding success for males and females from the 1971–80 cohorts, which had completed their reproductive life span by the time of this analysis. For each cohort, the mean and variance in breeding success were calculated across all members of each sex that survived to at least 2 years. (a) Cohort mean breeding success in relation to total April and May rainfall (mm) in the cohorts' year of birth. (b) The variance in breeding success for different cohorts: □, males; ◇, females.

members that survived to two years was not related to cohort mean breeding success ( $F_{1,8} = 1.02$ ,  $P = 0.343$ ). Similarly, there was no association between any of our measures of adult body size and cohort breeding success: hind foot length ( $F_{1,8} = 0.02$ ,  $P = 0.905$ ); jaw length ( $F_{1,8} = 0.00$ ,  $P = 0.964$ ); body weight ( $F_{1,8} = 0.79$ ,  $P = 0.400$ ).

#### SEX DIFFERENCES IN COHORT SURVIVAL AND BREEDING SUCCESS

Cohort variation was more extreme amongst males than females, both for breeding success and survival. Female survival through the first summer ranged between 0.73 and 1.00 and was significantly greater than male survival through the same period (Median values: males ( $n = 22$ ) 0.86, females ( $n = 22$ ) 0.91; Mann–Whitney  $U$  test:  $U = 150$ ,  $z = -2.159$ ,  $P = 0.030$ ). Likewise, winter survival of female calves ranged between 0.60 and 1.00 and was significantly

greater than male calf winter survival (Median values: males ( $n = 22$ ) 0.77, females ( $n = 22$ ) 0.91; Mann–Whitney test  $U = 138.5$ ,  $z = -2.429$ ,  $P = 0.015$ ). Following the first year of life, there were no significant sex differences in survival (Yearling calf survival: median values: males ( $n = 21$ ) 0.93, females ( $n = 21$ ) 0.93; Mann–Whitney test:  $U = 201.5$ ,  $z = -0.731$ ,  $P = 0.465$ ; adult survival: median values: males ( $n = 15$ ) 0.78, females ( $n = 15$ ) 0.87; Mann–Whitney test:  $U = 90.5$ ,  $z = -0.914$ ,  $P = 0.361$ ).

Breeding success was also significantly more variable in males than in females and the variance amongst males exceeded that for females by more than 3 (Fig. 3b;  $F_{1,18} = 5.14$ ,  $P = 0.036$ , one-way ANOVA).

## Discussion

Our study is the first to explore variation between cohorts in both male survival and reproduction. We describe significant variation in cohort survival, related to environmental conditions in the cohorts' year of birth: calf survival through the first winter decreased as female population density increased; yearling survival through the second year was lower for late-born cohorts. Adult survival was significantly higher for late-born cohorts and for cohorts born at high population density. In addition, cohorts which experienced high juvenile mortality in the first 2 years subsequently experienced high adult survival.

Survival through the first winter was density-dependent in both sexes, but the environmental parameters related to cohort differences in survival differed between the sexes: the timing of birth was influential amongst males but not females (Albon *et al.* 1987). More importantly, cohort survival through the first year of life was significantly lower for males than females, supporting the prediction that cohort effects will be more extreme amongst males than females.

Mean breeding success also varied significantly between cohorts, in relation to environmental conditions in the cohorts' year of birth: cohorts born in wet springs had higher mean breeding success. Here, also, there were significant differences with previous observations on females (Albon *et al.* 1987). Different parameters determined breeding success amongst males (rainfall) and females (temperature). Moreover, the variance in male cohort breeding success was more than three times greater than that in females, supporting the prediction that cohort variation will be more pronounced amongst males than females.

We expected to observe a positive relationship between early development and cohort body size, survival and breeding success, which would lead to selection (Darwin 1859; Darwin 1871; Trivers 1972; Lande 1981). However, we found no evidence for any relationship with differences in survival or breeding success between cohorts, in either birth weight or adult hind foot length, jaw length and body weight, all of which are known to be under direct positive selection

amongst individuals (Clutton-Brock *et al.* 1988; Rose 1995). These results imply that, contrary to our expectations, cohort variation might have limited consequences for natural or sexual selection in free-ranging populations.

Our observations were consistent with the action of density-dependent selection, or 'self-thinning', within cohorts (Yoda *et al.* 1963; Begon *et al.* 1986; Elliott 1993). Cohorts that suffered high juvenile mortality subsequently showed significantly higher adult survival (Fig. 1e). There is growing evidence that density-related selection within cohorts can produce such patterns of survival. For example, when young salmonoids *Salmo trutta* have undergone strong density-dependent competition so that survival rates are low, their subsequent survival is higher than that of fish not subjected to strong density-dependent selection during their early development (Elliott 1996). Although the patterns of survival described above support the action of density-dependent selection in our population, the density–weight relationship (the 'thinning line') differed significantly from the predicted value of  $-1.33$  (Begon *et al.* 1986), for five of the six cohorts we examined (Fig. 2). However, as thinning lines are estimated in more animal populations, it is becoming apparent that they almost invariably differ from  $-1.33$  (Begon *et al.* 1986; Elliott 1993; Armstrong 1997). Consequently, Armstrong (1997) suggests that, rather than estimating the gradient of the density–weight relationship, a conclusive demonstration of density-dependent selection requires measurement of population structure and processes, such as the mortality patterns described above and by Elliott (1996).

Our results have implications for the management of red deer and other ungulates where populations are managed to maximize the numbers of males that can be culled each year. If cohorts of males that show high juvenile survival show low adult survival, supplementary feeding could be used to offset the increased mortality. Observations from Norwegian populations of red deer, which are not food limited (Albon *et al.* 1992), suggest that supplementary feeding would reduce or remove cohort variation altogether. In those populations, 2- and 3-year-old females demonstrate significant variation in fecundity, but no such variation remains after females reach 4 years of age since individuals can compensate for early nutritional deficits (Albon *et al.* 1992).

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## References

- Albon, S.D. & Clutton-Brock, T.H. (1988) Temporal variation in climate and the population dynamics of red deer in Scotland. *Ecological Changes in the Uplands* (eds M.B. Usher & D. Thompson), pp. 93–107. Blackwell Science, Oxford.
- Albon, S.D., Clutton-Brock, T.H. & Guinness, F.E. (1983) The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). *Journal of Zoology*, **200**, 295–298.
- Albon, S.D., Clutton-Brock, T.H. & Guinness, F.E. (1987) Early development and population dynamics in red deer. 2. Density-independent effects and cohort variation. *Journal of Animal Ecology*, **56**, 69–81.
- Albon, S.D., Clutton-Brock, T.H. & Langvatn, R. (1992) Cohort variation in reproduction and survival: implications for population demography. *The Biology of Deer* (ed. D. Brown), pp. 15–21. Springer-Verlag, New York.
- Armstrong, J.D. (1997) Self-thinning in juvenile sea trout and other salmonid fishes revisited. *Journal of Animal Ecology*, **66**, 519–526.
- Begon, M., Firbank, L. & Wall, R. (1986) Is there a self-thinning rule for animal populations? *Oikos*, **46**, 122–124.
- Borgerhoff Mulder, M. (1988) Reproductive success in three Kipsigis cohorts. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 419–439. University of Chicago Press, Chicago.
- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M. & Guinness, F.E. (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour*, **27**, 211–225.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1982) *Red Deer – Behaviour and Ecology of Two Sexes*. University of Chicago Press, Chicago.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1988) Reproductive success in male and female red deer. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 325–343. University of Chicago Press, London.
- Clutton-Brock, T.H., Major, M., Albon, S.D. & Guinness, F.E. (1987) Early development and population dynamics in red deer. 1. Density-dependent effects of juvenile survival. *Journal of Animal Ecology*, **56**, 53–67.
- Clutton-Brock, T.H., Major, M. & Guinness, F.E. (1985) Population regulation in male and female red deer. *Journal of Animal Ecology*, **54**, 831–846.
- Crawley, M.J. (1994) *GLIM for Ecologists*. Blackwell Science, Oxford.
- Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*. John Murray, London.
- Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*. John Murray, London.
- Elliott, J.M. (1993) The self-thinning rule applied to juvenile sea-trout, *Salmo trutta*. *Journal of Animal Ecology*, **62**, 371–379.
- Elliott, J.M. (1996) The relationship between smolt density and fry density in salmonoids. *Journal of Fish Biology*, **48**, 1030–1032.
- Genstat, 5 Committee (1993) *Genstat Release 5 Reference Manual*. Clarendon, Oxford.
- Glucksman, A. (1974) Sexual dimorphism in mammals. *Biological Reviews*, **49**, 423–475.
- Guinness, F.E., Albon, S.D. & Clutton-Brock, T.H. (1978a) Factors affecting reproduction in red deer (*Cervus elaphus*). *Journal of Reproduction and Fertility*, **54**, 325–334.
- Guinness, F.E., Clutton-Brock, T.H. & Albon, S.D. (1978b) Factors affecting mortality in red deer. *Journal of Animal Ecology*, **47**, 817–832.
- Harper, J.L. (1977) *The Population Biology of Plants*. Academic Press, London.
- Lande, R. (1981) Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Science, U.S.A.*, **78**, 3721–3725.
- McCleery, R.H. & Perrins, C.M. (1988) Lifetime reproductive success of the great tit, *Parus major*. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 136–154. University of Chicago Press, London.
- van Noordwijk, A.J. & van Balen, J.H. (1988) The great tit, *Parus major*. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 119–135. University of Chicago Press, London.
- Partridge, L. (1988) Lifetime reproductive success in *Drosophila*. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 11–23. University of Chicago Press, London.
- Pemberton, J.M., Albon, S.D., Guinness, F.E., Clutton-Brock, T.H. & Dover, G.A. (1992) Behavioural estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behavioural Ecology*, **3**, 66–75.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Rose, K.E. (1995) *Factors affecting lifetime reproductive success in red deer stags* (*Cervus elaphus*). PhD Thesis, University of Cambridge.
- Sedinger, J.S. & Flint, P.L. (1995) Environmental influence on life-history traits: growth, survival and fecundity in black brant (*Branta bernicla*). *Ecology*, **76**, 2404–2414.
- Seigel, S. & Castellan, N.J. (1988) *Nonparametric Statistics for the Behavioural Sciences*. McGrawHill, New York.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. Freeman & Co., New York.
- Stevenson, I.R. (1994) *Male-biased mortality in Soay sheep*. PhD Thesis, University of Cambridge.
- Suttie, J.M. & Mitchell, B. (1983) Jaw length and hind foot length as measures of skeletal development of red deer (*Cervus elaphus*). *Journal of Zoology, London*, **200**, 431–434.
- Trivers, R.L. (1972) Parental investment and sexual selection. *Sexual Selection and the Descent of Man 1871–1971* (ed. B. Campbell), pp. 136–179. Heinemann, London.
- Westoby, M. (1984) The self-thinning rule. *Advanced Ecological Results*, **14**, 167–225.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, H. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology of Osaka City University*, **14**, 107–129.

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