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Density-Independent Effects and Cohort Variation**

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EARLY DEVELOPMENT AND POPULATION DYNAMICS IN RED DEER. II. DENSITY-INDEPENDENT EFFECTS AND COHORT VARIATION

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SUMMARY

(1) We investigated cohort differences in survival and reproductive success of female red deer in an increasing population on the Isle of Rhum, Scotland.

(2) Juvenile survival and fecundity were density-dependent and showed a progressive decline in each successive cohort recruited into the population. In contrast, cohort differences in the survival of offspring were density-independent. After accounting for the density-dependent decline in fecundity, the residual variation of cohorts was concordant with the density-independent variation in survival of their offspring.

(3) Cohort differences in offspring survival were related to variation in mean birth weight of offspring born to the cohort. Cohort variation in offspring birth weight was correlated with differences in the cohort's birth weight. This, in turn, was positively correlated with temperature in April and May, the last 2 months of gestation.

(4) Cohorts born after warm springs were more likely to begin their breeding lives early and experienced higher adult survival rates than cohorts born after cold springs.

(5) The results suggest that early growth and development have a permanent effect on reproductive success presumably because the prevailing environmental conditions in the first summer of life influence adult size. The implications of these density-independent effects for population demography and reproductive strategies are discussed.

INTRODUCTION

In red deer, as in other mammals, an individual's birth weight is closely related to its chances of surviving through its first year of life (Guinness, Clutton-Brock & Albon 1978; Clutton-Brock *et al.* 1987). Variation in birth weight may also have protracted effects since, in domestic mammals, man and red deer, it is known to influence adult body size and reproductive performance (Doney & Gunn 1981; Bongaarts & Potter 1983; Clutton-Brock, Albon & Guinness 1987). Annual variation in birth weight (Albon, Guinness & Clutton-Brock 1983) might consequently be expected to generate differences in survival and reproductive performance between cohorts. If pronounced, as is likely in food-limited populations of wild animals, cohort differences in survival and reproductive success may have an important influence on the population dynamics (see Grubb 1974) as well as the reproductive strategies of individuals (Werren & Taylor 1984).

In the previous paper (Clutton-Brock *et al.* 1987) we described density-dependent changes in juvenile survival of red deer. In this paper, we investigate the extent and causes of cohort variation in juvenile and adult survival as well as in fecundity, offspring birth weights and offspring survival among cohorts of red deer born since 1964 on the Isle of Rhum, Scotland.

Cohort variation in red deer

TABLE 1. Survival rates of females born into different cohorts since 1969. Juvenile survival is measured over the first 2 years of life and also subdivided into summer calf survival, winter calf survival and yearling survival. Adult survival is calculated as an annual survival rate, age 2 through 8 years (see Caughley 1977)

Cohort	No. of females born	Population size (females \geq 1 year)	Mean birth wt. of cohort (kg)	Juvenile survival					Annual adult survival rate 2-8 years
				Total 0-24 months	Calf summer 0-4 months	Calf winter 5-12 months	Yearling 13-24 months	Yearling 13-24 months	
1969	—	—	—	—	Data incomplete			0.962	
1970	7	50	5.47	—	Data incomplete			0.936	
1971	10	57	6.22	0.889	1.000	1.000	0.889	1.000	
1972	13	66	6.72	1.000	1.000	1.000	1.000	0.956	
1973	18	77	—	0.889	0.944	1.000	0.941	0.955	
1974	25	90	6.78	0.800	0.920	0.913	0.952	0.973	
1975	22	106	6.48	0.727	0.909	0.800	1.000	0.933	
1976	26	117	6.09	0.517	0.731	0.789	1.000	0.977	
1977	22	128	5.56	0.636	0.909	0.950	0.737	0.914	
1978	23	140	6.36	0.652	0.870	0.850	0.882	Data incomplete	
1979	28	150	5.46	0.643	0.929	0.923	0.750	Data incomplete	
1980	31	160	6.83	0.580	0.903	0.714	0.900	Data incomplete	
1981	27	163	6.92	0.427	0.889	0.600	0.800	Data incomplete	
1982	28	162	6.36	0.679	0.929	0.769	0.950	Data incomplete	
1983	42	166	5.90	0.558	0.907	0.667	0.923	Data incomplete	

MATERIALS AND METHODS

The data used in this analysis were the same as those used in the previous paper (Clutton-Brock *et al.* 1987). In analyses of cohort differences in birth weight, juvenile survival, adult survival and age at first breeding, we calculated average values for all animals belonging to each cohort (Table 1). However, when investigating cohort differences in fecundity and offspring survival, it was necessary to control for the effects of maternal age, which is known to affect both variables (Guinness, Albon & Clutton-Brock 1978; Guinness, Clutton-Brock & Albon 1978) since our data did not cover the entire lifespans of all cohorts (see Table 1). To accomplish this, we used logistic models (Cox 1970; Clutton-Brock *et al.* 1987). Fecundity and offspring survival were recorded as binary variables: 0 if the hind failed to produce or the offspring died, 1 if the hind was fecund or the offspring survived. Binary dependent variables can be related to any metric independent variable by a logistic curve and this technique allowed us to calculate, for each cohort, a probability of fecundity or offspring survival that controlled for age variation.

Logistic models were inappropriate for analysis of continuous dependent variables such as birth weight and for this we used analysis of covariance (Snedcor & Cochran 1967) instead. When calculating values of offspring birth weight for each cohort, we controlled for the effects of three variables known to affect birth weight (Clutton-Brock, Guinness & Albon 1982): the mother's age, the sex of the offspring and its year of birth.

The analysis used data from twenty different cohorts born between 1964 and 1983. However, records for early and late cohorts were incomplete and it was necessary to restrict some analyses to smaller numbers of cohorts. For example, data on juvenile survival were not available before 1971, while cohorts born after 1979 had not been recruited to the breeding population and therefore we had no information on adult

fecundity for the 1980–83 cohorts. The cohorts used in each analysis are shown in the relevant figures and tables. Population density increased during the period of data collection (Clutton-Brock *et al.* 1987) and some of our analyses control for it by examining the residual variation left after density-dependent effects have been removed. The following variables were used in the analysis.

Cohort. All females (hinds) born in a given year in the study area.

Cohort birth weight. The mean weight at birth of all female calves born in a given year. Birth weight was calculated for all calves caught up to 2 weeks old. For calves caught after their day of birth we assumed a weight gain of 0.36 kg day^{-1} (Guinness, Albon & Clutton-Brock 1978). Since the age structure of the population differed between years and maternal age influences birth weight, we standardized the means as if all mothers were 7 years old when investigating cohort differences in birth weight.

Cohort survival (juveniles). The proportion of female calves belonging to the same cohort surviving to 2 years of age. Cohort survival as juveniles could be subdivided into three phases. (i) Summer calf survival: the proportion surviving from May to 1 October. (ii) Winter calf survival: the proportion of calves alive at the beginning of the winter (October) that survived until 30 April. (iii) Yearling survival: the proportion of hinds surviving from 13 to 24 months.

Cohort survival (adults). The annual survival rate of the cohort calculated from 2 to 8 years (see Caughley 1977).

Proportion of hinds fecund at 3 years old. The proportion of hinds in the cohort that calved for the first time as 3-year olds. Hinds usually calved for the first time as 3, 4 or 5-year olds.

Milk hind fecundity of cohort. The probability of hinds calving when milk, controlling for age effects. A milk hind was a female who had reared a calf through the previous summer and had therefore borne the costs of lactation.

Yield hind fecundity of cohort. The probability of hinds calving when yield. A yield hind was a multiparous hind that had either failed to calve the previous year or had lost her calf before October.

Mean birth weight of calves born to cohort. The average birth weight of offspring born to a cohort corrected for mother's age, sex of offspring and year of birth.

Survival of offspring born to cohort. The survival of offspring born to the cohort, controlling for the effects of maternal age. Survival of offspring born to each cohort was subdivided into three phases: summer calf survival, winter calf survival and yearling survival (see above).

RESULTS

Cohort differences in birth weight

The mean birth weight of female calves varied between years from 5.94 kg to 7.47 kg ($F_{11, 204} = 2.595$, $P < 0.005$). In contrast to most other measures of reproductive performance, birth weight did not decline with increasing density (Clutton-Brock *et al.* 1987) but was significantly correlated with mean daily temperature in April and May ($r = 0.658$, $t_{10} = 2.761$, $P < 0.05$; $Y = 3.58 + 0.371x$), the 2 months preceding birth (Fig. 1).

Cohort survival (juveniles)

Though the survival to 2 years of female juveniles varied significantly between the thirteen cohorts born between 1971 and 1983 from 1.00 to 0.427 ($\text{chi-squared}_{12} = 28.7$,

Cohort variation in red deer

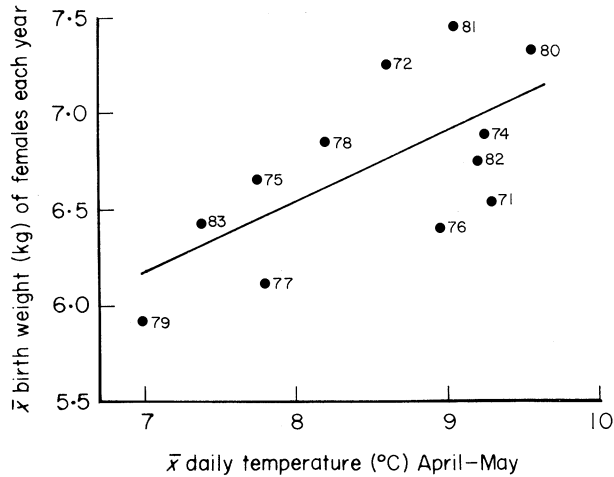


FIG. 1. The birth weight of cohorts of female red deer plotted against the mean daily temperature in April and May immediately prior to birth in June (Regression line $y = 3.58 + 0.371x$; $r = 0.658$, $F_{1,10} = 7.623$, $P < 0.05$).

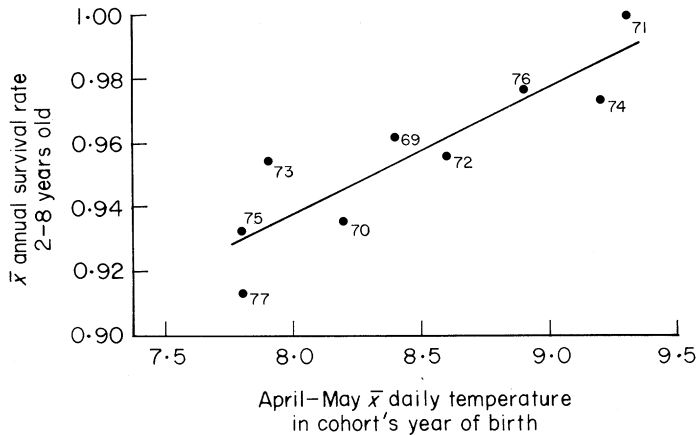


FIG. 2. The annual adult (2-8 years) survival rate of cohorts of female red deer plotted against the mean daily temperature in April and May in the cohort's year of birth (regression line $y = 0.623 + 0.39x$; $r = 0.884$, $F_{1,7} = 24.93$, $P < 0.01$).

$P < 0.01$), differences in survival through the first summer, first winter and second year of life were not concordant across cohorts (chi-squared₁₂ = 13.769, N.S., see Table 1). The survival of females during the first summer of life did not vary significantly (chi-squared₁₂ = 13.0, N.S.) and averaged 0.91 ± 0.066 S.E. It was not significantly related to population density ($r = -0.405$, N.S.). There was no consistent relationship between survival through the first summer and the mean birth weight of the cohort ($r = -0.200$, N.S.).

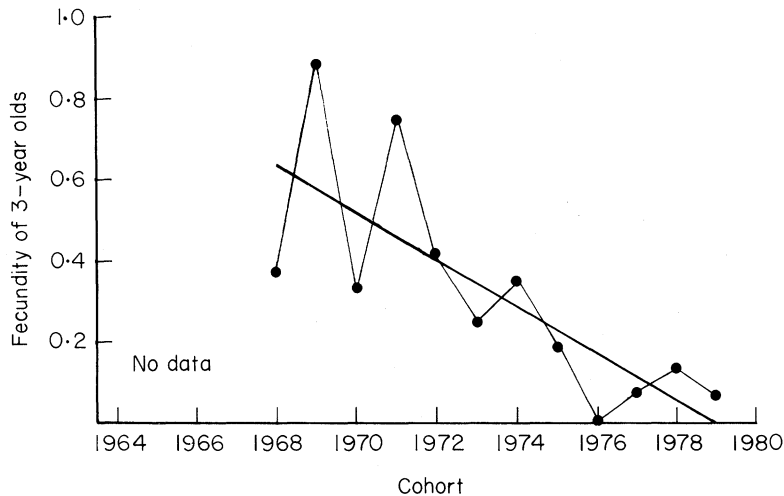


FIG. 3. The fecundity of 3-year olds born between 1968 and 1979. The regression line ($y = 0.91 - 0.11x$, where x (1964) = 1, $r = -0.762$, $F_{1,10} = 13.846$, $P < 0.01$) illustrates the overall trend.

The survival of females during the first winter varied significantly between cohorts (chi-squared₁₂ = 34.7, $P < 0.001$) from 1.0 (1971, 1972 and 1973 cohorts) to 0.60 (1981 cohort) (Table 1). Survival over the first winter declined significantly as population size increased ($r = -0.766$, $t_{11} = 3.957$, $P < 0.01$). It was not significantly correlated with birth weight ($r = -0.284$, N.S.).

Although yearling survival varied between cohorts from a probability of 1.0 (1972, 1975 and 1976 cohorts) to 0.74 (1977 cohort) (Table 1) these differences were not quite significant (chi-squared₁₂ = 18.7, $0.1 > P > 0.05$). Yearling survival did not decline significantly as the population increased ($r = -0.403$, N.S.). Although the two cohorts with the lowest birth weights exhibited the lowest survivorship there was no significant relationship across all the cohorts ($r = 0.288$, N.S.).

Although the three components of juvenile survival were not closely related to each other, juvenile survival calculated over the entire period between birth and 2 years showed a consistent decline as population density increased ($r = -0.881$, $t_{11} = 6.176$, $P < 0.001$).

Cohort survival (adults)

The annual survival rate of age 2–8 years measured for cohorts born between 1969 and 1977 varied from 1.0 (1971 cohort) to 0.91 (1977 cohort) (Table 1). The small differences between cohorts were not significantly correlated with juvenile survival ($r = 0.238$, N.S.) population size ($r = -0.369$, N.S.) or mean birth weight of the cohort ($r = 0.463$, N.S.). However, cohort differences in annual adult survival rate were significantly correlated to mean daily temperature in April and May in the cohort's year of birth ($r = 0.884$, $t_7 = 4.993$, $P < 0.01$, see Fig. 2).

Fecundity of cohort

The fecundity of 3-year old breeders (Fig. 3: $r = -0.762$, $t_{10} = 3.72$, $P < 0.01$) and milk hinds (Fig. 4: $r = -0.761$, $t_{14} = 4.389$, $P < 0.01$) in successive cohorts declined with increasing population density. No change occurred in the fecundity of yield hinds. In milk

Cohort variation in red deer

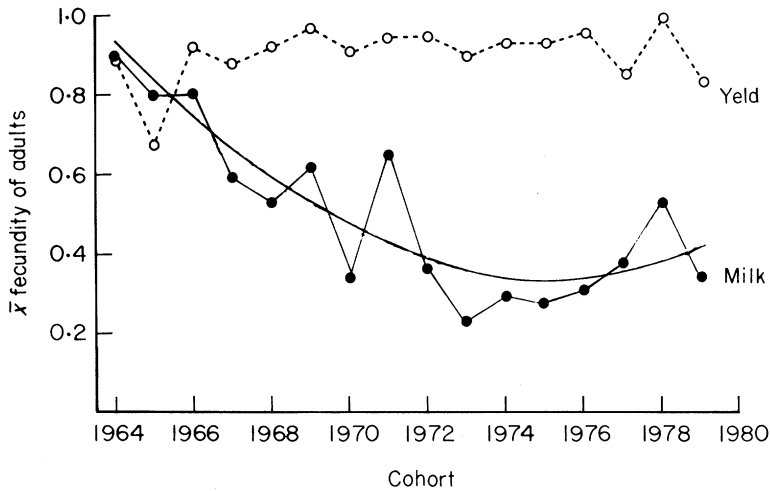


FIG. 4. The fecundity of adults by cohort and separated according to whether they were previously milk or yield. The polynomial curve ($y = 1.03 - 0.116x + 0.00486x^2$ where x (1964) = 1, $r^2 = 0.746$, $F_{2,13} = 23.024$, $P < 0.001$) illustrates the overall trend in milk hind fecundity.

hinds a quadratic curve significantly improved the fit to the data (reduction in sums of squares by inclusion of x^2 ; $F_{1,12} = 11.882$, $P < 0.01$).

There were substantial differences in mean fecundity between successive cohorts which were consistent in different categories of hinds (Figs 3, 4). The residuals for 3-year old and milk hinds were significantly correlated with each other ($r = 0.786$, $t_{10} = 4.016$, $P < 0.01$). For example, the 1969, 1971 and 1978 cohorts had higher than average fecundity while the 1970 and 1973 cohorts showed lower fecundity than expected. Cohort differences in fecundity were not related to the mean birth weight of the cohort (3-year olds: $r = 0.302$, N.S.; milk hinds: $r = 0.231$, N.S.). However, when we included the 1980, 1981 and 1982 cohorts which are the most recent recruits to the breeding population, we found that the residual variation in 3-year old fecundity was significantly related to April–May temperature in the cohort's year of birth (Fig. 5: $r = 0.639$, $F_{1,10} = 6.909$, $P < 0.05$).

Mean birth weight of calves born to cohort

The mean birth weight of calves born to different cohorts of hinds over their lifespans varied significantly between cohorts ($F_{15,429} = 6.342$, $P < 0.01$) and ranged from 5.05 kg (1970 cohort) to 7.30 kg (1966 cohort). It was significantly related to the mean birth weight of the cohort itself ($r = 0.705$, $t_7 = 2.630$, $P < 0.05$; Fig. 6).

Although cohort variation in offspring birth weight was related to differences in the cohort's own birth weight, 50% of the variance in offspring birth weight was left unaccounted for. The residual variation was significantly negatively correlated with the temperature in the cohort's first month of life (June) ($r = -0.689$, $t_7 = 2.516$, $P < 0.05$). Cohorts beginning life in warm June weather subsequently gave birth to smaller offspring than would have been predicted on the basis of their birth weight, while cohorts beginning life in cool June weather tended to have larger offspring (Fig. 7). In turn, the cohort's birth weight and mean daily temperature in the first month of life accounted for 73.6% of the variance in offspring birth weight between cohorts.

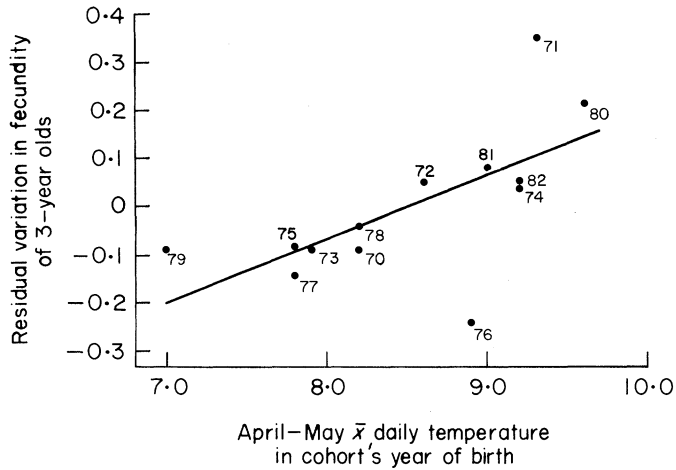


FIG. 5. The residual variation (see text) in 3-year old fecundity plotted against the mean daily temperature in April and May in the cohort's year of birth ($r=0.639$, $F_{1,10}=6.909$, $P<0.05$).

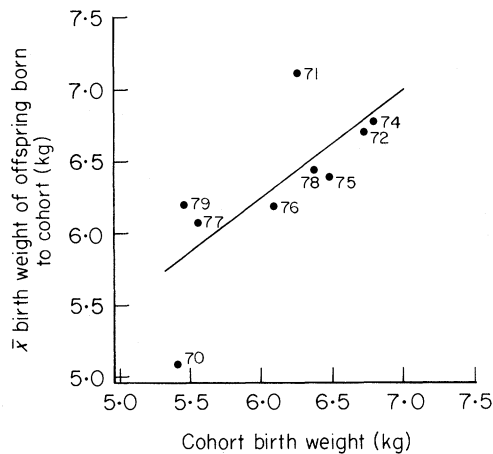


FIG. 6. Mean offspring birth weight of each cohort plotted against the cohort's own birth weight (regression line $y=1.687+0.76x$, $r=0.705$, $F_{1,7}=6.92$, $P<0.05$).

Cohort differences in offspring survival

There was no progressive decline in the survival of offspring born to successive cohorts recruited to the breeding population (Fig. 8). Cohort differences in the survival of offspring through the summer were smaller than survival through the first winter or as yearlings and although they ranged from 0.70 for the 1970 cohort to 0.95 for the 1971 cohort these differences were not significant ($\chi^2_{15}=22.7$, $P>0.05$). In contrast, offspring survival through the first winter differed significantly between cohorts ($\chi^2_{15}=26.8$, $P<0.05$) ranging from 0.48 (1970 cohort) to 0.88 (1979 cohort). Differences in offspring survival as yearlings were also pronounced ($\chi^2_{15}=31.6$, $P<0.01$), ranging from 0.62 (1973 cohort) to 1.00 (1977 cohort). Cohort differences in

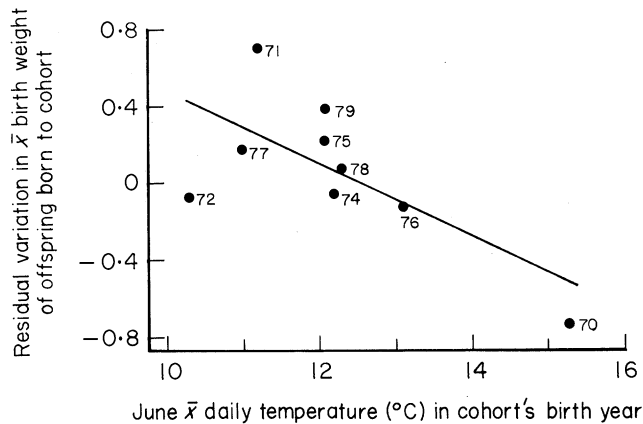


FIG. 7. The residual variation about the relationship between mean offspring birth weight and the cohort's own birth weight (Fig. 4) plotted against June mean daily temperature in the cohort's birth year (Regression $y = 2.353 - 0.188x$, $r = -0.689$, $F_{1,7} = 6.330$ $P < 0.05$).

offspring survival through the first winter and as yearlings were intercorrelated ($r = 0.554$, $t_{14} = 2.491$, $P < 0.05$) but neither was closely related to cohort differences in offspring survival through the first summer (winter calf survival, $r = 0.472$, $t_{14} = 2.002$, $0.1 > P > 0.05$; yearling survival: $r = 0.196$, N.S.).

Cohort differences in offspring survival between birth and 2 years were positively correlated with the mean birth weight of offspring born to the cohort ($r = 0.668$, $t_{14} = 3.547$, $P < 0.01$: see Fig. 9). Cohort variation in fecundity was also related to variation in offspring birth weight ($r = 0.524$, $t_{14} = 2.305$, $P < 0.05$) though the relationship was presumably not a causal one. As we have already described, offspring birth weight was related to both the cohort's mean birth weight and temperature in their first month of life.

Cohort differences in reproductive rate

Though not all the five components of reproductive success that we examined were closely inter-correlated, differences between cohorts were concordant (Kendall's coefficients of concordance = chi-squared₁₁ = 30.74, $P < 0.01$, Tables 2, 3). As a result, inter-cohort differences in the production of surviving offspring were pronounced, ranging from 0.073 offspring per year for the 1970 cohort to 0.372 offspring per year for the 1971 cohort. (Because of the density-dependent decline in fecundity, values were standardized and expressed relative to the variation in 1983.)

DISCUSSION

Our analysis has demonstrated significant differences in juvenile survival rates and adult reproductive success between cohorts of female red deer. The probability of survival over the first 2 years of life differed between cohorts from 0.427 to 1.00 while the mean number of surviving offspring produced per year by adults reaching breeding age ranged from 0.073 to 0.372, a factor of five.

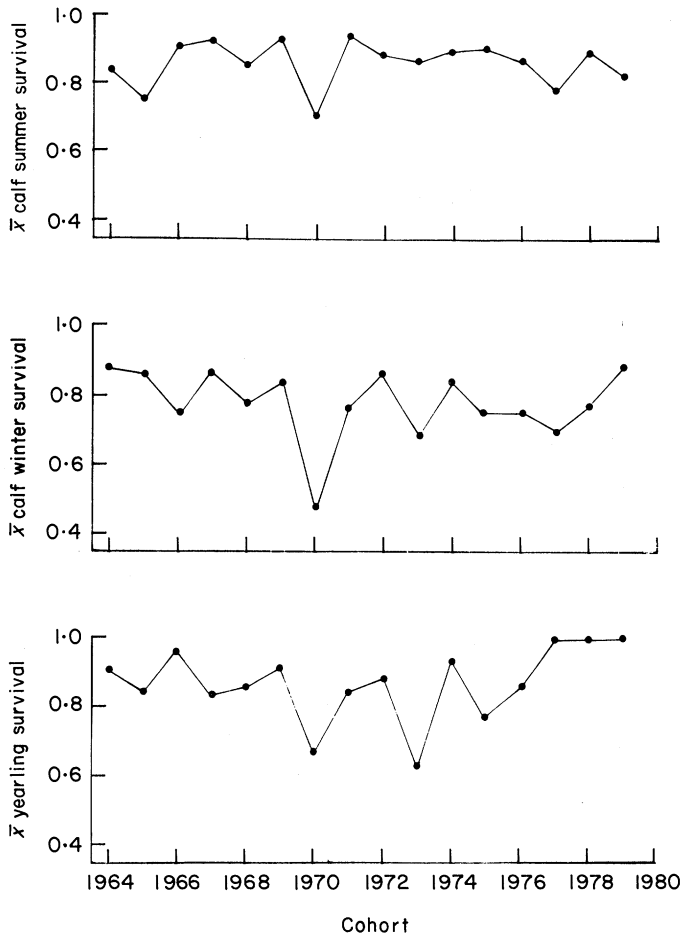


FIG. 8. Differences between cohorts in the probability of their offspring surviving as (a) calves through the first summer (b) calves through the first winter and (c) yearlings.

As the population size trebled successive cohorts showed a density-dependent decline in survival as juveniles and in fecundity as adults. In contrast, cohort differences in offspring survival were not related to population density. After accounting for the density-dependent decline in fecundity the residual variation was correlated with cohort differences in offspring survival, such that the offspring of the most fecund cohorts were also more likely to survive the three phases in which juvenile mortality occurred. Cohort differences in offspring survival were correlated with the mean birth weight of offspring born to the cohort. In turn, offspring birth weight varied in relation to the cohort's own birth weight, which depended on mean daily temperature in the spring immediately prior to birth. Presumably the influence of mean daily temperature in April and May on birth

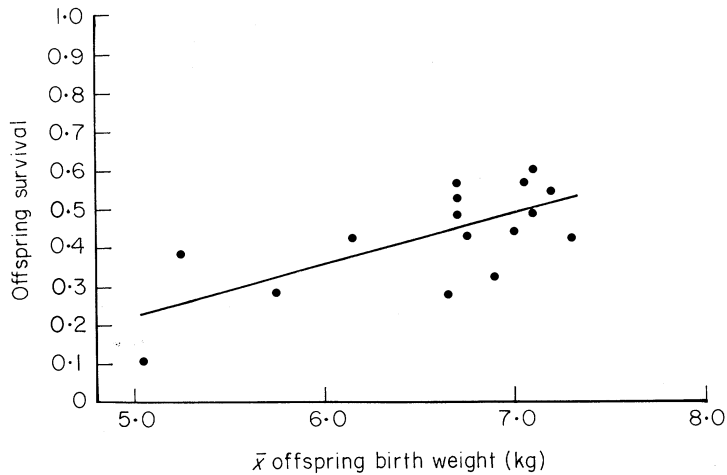


FIG. 9. Offspring survival to 2 years of age plotted against the mean offspring birth weight of the cohort (Regression line $y = 0.13x - 0.42$, $r = 0.668$, $F_{1,14} = 12.581$, $P < 0.01$).

TABLE 2. Measures of fecundity and offspring survival ranked across cohorts (1968–79) to illustrate the concordance of components of reproductive success. The absolute values are shown in Fig. 2, 3 and 6

Cohort	Fecundity		Offspring survival			Rank of average of ranks
	3-year olds	Milk hinds	Calf summer	Calf winter	Yearling	
1968	1	6	4	8	5.5	3.5
1969	12	10	11	10	8	12
1970	2	2	1	1	2	1
1971	11	12	12	6	4	11
1972	7	8	7	11	7	8.5
1973	4	1	6	2	1	2
1974	9	4	8	9	9	7
1975	5	3	10	5	3	5
1976	3	7	5	4	5.5	3.5
1977	6	9	2	3	10.5	6
1978	10	11	9	7	10.5	10
1979	8	5	3	12	12	8.5

weight accounts for the relationship of both residual variation in 3-year old fecundity and adult survival rate with April–May temperature. The lack of a direct relationship between adult survival rates and the cohort's own birth weight may be due simply to the apparently aberrant value for 1971 in such a small sample size.

The cause of the positive association between spring temperature and birth weight was presumably that the timing of the first flush of spring growth affects the nutritional status of pregnant hinds (Albon, Guinness & Clutton-Brock 1983), thereby influencing foetal growth (Robinson 1977). The relationship between cohort differences in birth weight and

TABLE 3. Pearson product-moment correlations between measures of fecundity and offspring survival for different cohorts. The matrix shows correlations across cohorts 1968 to 1979

		3 year olds				
Fecundity	Milk hinds	0.786 **	—			
	Calf summer	0.597 *	0.494 NS	—		
Offspring survival	Calf winter	0.480 NS	0.424 NS	0.698 *	—	
	Yearling	0.396 NS	0.587 *	0.191 NS	0.658 *	—
		3-year olds	Milk hinds	Summer	Winter calf	Yearling
		Fecundity		Offspring survival		

* $P < 0.05$ ** $P < 0.01$.

those in offspring birth weight was probably caused by effects of the cohort's birth weight on the growth and adult body size of its members, for individual differences in birth weight are correlated with adult weight in the same population (Clutton-Brock, Albon & Guinness 1987). Whether low birth weight affects adult size and reproductive performance directly or whether low birth weight initiates a chain of separate causal relationships cannot be determined from our data. The close association between the average birth weight of offspring born to different cohorts over their members' lifespans and inter-cohort differences in offspring survival agrees with the extensive evidence that birth weight exerts a strong effect on juvenile survival in wild ungulates (Grubb 1974; Clutton-Brock *et al.* 1982, 1987).

Our analysis produced three anomalies. First, why should climatic factors in the year of birth be the principal determinant of annual variation in birth weight whereas the birth weight of the mother is the principal determinant of inter-cohort differences in offspring birth weight? In this case, the anomaly is illusory. Climatic factors during the year of birth may be the principal cause of annual variation in birth weight but may have little or no effect on inter-cohort variation because, over their lifetime, most hinds breed in good as well as in bad seasons and the average spring climate experienced by different cohorts over their lifespans may vary little.

Second, why should calf birth weight be positively related to mean daily temperature in April and May, while cohorts that experience relatively high temperatures in their first month of life (June) produce lighter calves as adults than would be expected from their own birth weights? The likely explanation is that while warm weather in early spring advances the onset of the growing season, higher than average temperatures in summer are generally associated with reduced precipitation or higher rates of evapo-transpiration (see Munro & Davies 1973). Even in the wet environment of the West Highlands, annual variation in summer rainfall influenced the proportion of time hinds spent feeding on the most nutritious vegetation communities (Clutton-Brock *et al.* 1982) and also their body weight in the autumn (Albon 1983). It would, consequently, not be surprising if high summer temperatures reduced the growth rates of young animals, thus affecting their adult size and reproductive performance. A similar tendency for the autumn weights of calves, yearlings and adults to be negatively related to summer temperature has been found in Norwegian moose population (Saether 1985).

Third, why should cohort differences in survival during the first 2 years of life and in fecundity in adulthood vary with population density while cohort differences in offspring birth weight and offspring survival vary in a density-independent manner with the cohort's own birth weight? The most likely explanation appears to be that high population density depresses food availability in summer, thus affecting juvenile survival and fecundity the following autumn. Its effects on birth weight may be relatively slight because food availability in early spring and foetal growth are more strongly affected by the timing of the start of spring growth than by competition for food during the winter months, when hinds are feeding on relatively abundant foods of low nutritional quality (Clutton-Brock, Guinness & Albon 1982). The close relationship between birth weight, adult size and offspring birth weights suggests that an individual's birth weight may influence its subsequent growth trajectory, exerting a stronger effect on its adult size than resource availability during its first year of life. We are currently investigating this surprising conclusion.

Our results show that the effects of early development on size and reproductive performance in adulthood are substantially stronger in wild red deer than the literature on domestic species would suggest (Gunn 1968; Allden 1970; Doney & Gunn 1981). This is presumably because intense competition for resources maintains or exaggerates initial differences in growth and resource access (T. H. Clutton-Brock, S. D. Albon & F. E. Guinness, unpublished). Whether or not they are unusually strong in our population because they live close to the periphery of the species' range will only be determined by similar analyses for other interoparous vertebrates. However the presence of pronounced annual variation in average birth or juvenile body weights in other temperate mammals (Geist 1971; Grubb 1974) suggests that similar effects may be widespread.

The existence of pronounced differences in reproductive performance between successive cohorts has important implications for our understanding of the population biology of red deer. First, it indicates that a substantial proportion of individual variation in breeding success is not of genetic origin (T. H. Clutton-Brock, S. D. Albon & F. E. Guinness, unpublished). Second, it suggests that the reproductive strategies of individuals would be expected to vary between successive cohorts. In particular, selection pressures are likely to favour variation in offspring sex ratios between successive cohorts (Trivers & Willard 1973; Werren & Taylor 1984). And third, it predicts that population size and recruitment will continue to oscillate after populations have reached carrying capacity as good and bad cohorts progress through their lifespans.

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REFERENCES

- Albon, S. D. (1983). *Ecological aspects of growth, reproduction and mortality in female red deer*. Unpublished Ph.D. thesis, University of East Anglia.

- Albon, S. D., Guinness, F. E. & Clutton-Brock, T. H. (1983). The influence of climatic variation on the birth weights of red deer calves. *Journal of Zoology (London)*, **200**, 295–297.
- Allden, W. G. (1970). The effects of nutritional deprivation on the subsequent productivity of sheep and cattle. *Nutrition Abstracts & Reviews*, **40**, 1167–1184.
- Bongaarts, J. & Potter, R. G. (1983). *Fertility, Biology and Behaviour*. Academic Press, New York.
- Caughley, G. (1977). *Analysis of Vertebrate Populations*. Wiley, London.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1987). Reproductive success in male and female red deer. *Reproductive Success* (Ed. by T. H. Clutton-Brock), (in press). University of Chicago Press, Chicago.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago.
- Clutton-Brock, T. H., Iason, G. R., Albon, S. D. & Guinness, F. E. (1982). Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. *Journal of Zoology (London)*, **198**, 227–236.
- Clutton-Brock, T. H., Major, M., Albon, S. D. & Guinness, F. E. (1987). Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology*, **56**, 53–67.
- Cox, D. R. (1970). *The Analysis of Binary Data*. Methuen, London.
- Doney, J. M. & Gunn, R. G. (1981). Nutritional and other factors in breeding performance of ewes. *Environmental factors in mammal reproduction* (Ed. by D. Gilmore & B. Cook), pp. 169–177. Macmillan, London.
- Geist, V. (1971). *Mountain Sheep: A Study in Behaviour and Evolution*. University of Chicago Press, Chicago.
- Grubb, P. (1974). Population dynamics of the Soay sheep. *Island Survivors: The Ecology of Soay Sheep on St. Kilda* (Ed. by P. A. Jewell, C. Milner & J. M. Boyd), pp. 242–272. Athlone Press, London.
- Guinness, F. E., Albon, S. D. & Clutton-Brock, T. H. (1978). Factors affecting reproduction in red deer (*Cervus elaphus* L.). *Journal of Reproduction & Fertility*, **54**, 325–334.
- Guinness, F. E., Clutton-Brock, T. H. & Albon, S. D. (1978). Factors affecting calf mortality in red deer. *Journal of Animal Ecology*, **47**, 817–832.
- Gunn, R. G. (1968). Levels of first feeding in relation to performance of Cheviot hill ewes. VI. Life-time production from the hill. *Journal of Agricultural Science (Cambridge)*, **71**, 161–166.
- Munro, J. M. M. & Davies, D. A. (1973). Potential pasture production in the uplands of Wales. 2. Climatic limitations on production. *Journal of the British Grassland Society*, **28**, 161–169.
- Robinson, J. J. (1977). The influence of maternal nutrition on ovine foetal growth. *Proceedings of the Nutrition Society*, **36**, 9–16.
- Saether, B. E. (1985). Annual variation in carcass weight of Norwegian Moose (*Alces alces*) in relation to climate along a latitudinal gradient. *Journal of Wildlife Management*, **49**, 977–983.
- Snedecor, G. W. & Cochran, W. G. (1967). *Statistical Methods*, 6th edn. Iowa State University Press.
- Trivers, R. L. & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**, 90–92.
- Werren, J. & Taylor, P. D. (1984). The effects of population recruitment on sex ratio selection. *American Naturalist*, **124**, 143–148.

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