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Does environmental stochasticity matter? Analysis of red deer life-histories on Rum

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Summary

Most life-history theory assumes that short-term variation in an organism's environment does not affect the survivorships and fecundities of the organisms. This assumption is rarely met. Here we investigate the population and evolutionary biology of red deer, *Cervus elephas*, to see if relaxation of this assumption is likely to make significant differences to the predicted evolutionary biology of this species. To do this we used 21 years of data from a population of deer on Rum, Western Isles, Scotland. Population growth rates in a stochastic environment were estimated using Tuljapurkar's small noise approximation, confirmed by bootstrap simulation. Numerical differentiation was used to see if the selection pressures (i.e. sensitivities of population growth rate to changes in the vital rates) differ between the stochastic and deterministic cases. The data also allow the costs of reproduction to be estimated. These costs, incorporated as trade-offs into the sensitivity analysis, allow investigation of evolutionary benefits of different life-history tactics. Environmentally induced stochastic variation in the red deer vital rates causes a slight reduction ($\approx 1\%$) in the predicted population growth rate and has little impact on the estimated selection pressures on the deer's life-history. We thus conclude that, even though density-independent stochastic effects on the population are marked, the deer's fitness is not markedly affected by these and they are adapted to the average conditions they experience. However, the selected life-history is sensitive to the trade-offs between current fecundity, survivorship and future fecundity and it is likely that the environmental variance will affect these trade-offs and, thus, affect the life-history favoured by selection. We also show that the current average life-history is non-optimal and suggest this is a result of selection pressures exerted by culling and predation, now much reduced. As the use of stochastic or deterministic methods provide similar estimates in this case, the use of the latter is justified. Thus, r (the annual per capita rate of population growth) is an appropriate measure of fitness in a population with stochastic numerical fluctuations. In a population of constant size lifetime reproductive success is the obvious measure of fitness to use.

Keywords: stochastic demography; fitness; life-history; red deer; selection pressures; cost of reproduction

Introduction

Populations living in a constant environment will experience density-independent population growth at a rate given by r in the Euler–Lotka equation (Caswell, 1989). This equation is deterministic, in that fixed schedules of survivorship and fecundity will give a definite, determinable rate of population growth.

In the real world, however, survivorships and fecundities are not constant, but vary through time as the environment varies in a stochastic manner. When this occurs there is no pre-determined rate of population growth, only a probabilistic expectation of growth at a certain rate. The rate of population growth will almost always be less than in a deterministic environment. This is because the rate of population growth is essentially a geometric mean and variance reduces

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its magnitude. The reduction in growth rate caused by environmental stochasticity depends upon four factors (Orzack, 1985; Tuljapurkar, 1990a; Benton and Grant, in press): the magnitude of the variation, the pattern of co-variation between survivorship and fecundity variations, the autocorrelation between environmental states over time and the life-history of the organism concerned.

Population growth rates are often identified as 'fitness' (Charlesworth, 1980; Lande, 1982; Tuljapurkar, 1982; Metz *et al.*, 1992). In environments where there is environmentally induced stochastic variation in survivorships and fecundities, the stochastic population growth rate may often be a more appropriate measure of fitness in a variable environment than the more commonly used r or lifetime reproductive success. As different life-histories are differently affected by given amounts of variation, the 'fittest' life-history may differ between environments characterised by different variabilities. For example, it has long been known that variable environments (especially where juvenile mortality is more variable than adult mortality) may select for iteroparity in organisms, so-called bet-hedging (Murphy, 1968; Schaffer, 1974; Fox, 1993). However, semelparity may also be favoured by environmental variability (Orzack and Tuljapurkar, 1989; Tuljapurkar, 1990a). Variability may select for delayed reproduction such as occurs in insect diapause, seed dormancy, cohort splitting or delayed flowering in biennials (Tuljapurkar, 1990a,b). Variability may select phenotypic plasticity in some situations, but not others (Orzack, 1985).

Variability is therefore known to be capable of inducing profound effects on the evolutionary biology of organisms. These conclusions are, however, largely based on a number of theoretical studies, especially those conducted by Tuljapurkar and Orzack (op. cit.). The investigation of the impacts on the variability on real organisms has been thwarted by two main factors. First, the calculation of stochastic population growth rate is 'dauntingly technical' (Caswell, 1989). Second, to estimate growth rates with any precision requires knowledge of the way that organisms' vital rates vary through time; short-term studies rarely provide sufficient information even if this information is reported.

A population of red deer, *Cervus elephas* L., on the island of Rum off the west coast of Scotland, UK, has been intensively studied from 1969 to the present (Clutton-Brock *et al.*, 1982; Clutton-Brock and Albon, 1989; T.H. Clutton-Brock, unpublished). The deer live on the edge of the species' range, in an almost predator-free environment (culling has not occurred since 1972), though calves are sometimes attacked by golden eagles or gulls, especially if sickly (Clutton-Brock *et al.*, 1982). The weather is variable and has important consequences on the growth, survival, recruitment and reproduction of the deer (Albon and Clutton-Brock, 1988; Clutton-Brock and Albon, 1989, Chapter 6; Albon *et al.*, 1992). The dates of birth and death for all individuals in this population and their reproductive success have been continually monitored over this period. This dataset provides a unique opportunity to investigate the effects of stochastic variation on the population growth rates and selection pressures on the life-history of a long-lived mammal.

We calculate the stochastic population growth rate for the deer using two main methods (see below): an analytical approximation developed by Tuljapurkar (1982) and a numerical approximation. The comparison of these two estimates of population growth rate with the deterministic growth rate allows the impact of environmental stochasticity on fitness to be evaluated. Comparison of the two estimates of fitness in a stochastic environment also provides information on evaluating the usefulness of Tuljapurkar's (1982) approximation. The impact of environmental stochasticity on the deer's life-history can be investigated by examining the sensitivity of fitness to marginal changes in the life-history. This *sensitivity analysis* can be conducted assuming that the vital rates can be varied independently (e.g. Caswell, 1989). However, comparing the survivorship and fecundity the following year of reproductive females (milk hinds) and non-reproductive females (yeld hinds) allows the costs of reproduction to be

estimated. These costs can then be incorporated, as trade-offs, into the sensitivity analysis to provide a more realistic picture of the changes in fitness associated with changes in the female's life-history, both in a constant and stochastic environment.

Methods

Leslie matrix models

In this investigation we consider female deer only. We make extensive use of age-structured population matrix models; for an excellent introduction see Caswell (1989). We treat the population as a birth-pulse population (as all the young are born more or less synchronously in mid-summer), with an annual census occurring just prior to the females giving birth. For each year from 1971 to 1991 a Leslie or projection matrix was constructed. This takes the form

$$\begin{pmatrix} F_1 & F_2 & F_3 & \dots & F_n \\ S_1 & 0 & 0 & \dots & 0 \\ 0 & S_2 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & S_{n-1} & 0 \end{pmatrix}$$

where the F_x are the number of females born to each female of age x , that survive to the next census (i.e. at 1 year old) and the S_x are the probabilities of females of age x surviving to the next census (i.e. age $x + 1$). The matrices are of dimension 19. It should be noted that the F_x and S_x are population means so, although both are individually either 1 or 0 (either a female survives or dies or reproduces or does not), taken as a whole the population (or assumed genotype-specific) values can be treated as continuous variables. The year-specific matrices can be averaged to give a mean matrix for the whole period under study. Many of the common deterministic analyses utilize the eigenvectors associated with the dominant eigenvalue ($\lambda = e^r$) of this mean projection matrix (Caswell, 1989). The right eigenvalue, \mathbf{v} , is recognized as the asymptotic reproductive value of each age (or stage) considered in the mean matrix; the left, \mathbf{u} , is considered the stable age distribution. The magnitude of these eigenvectors for the mean matrix for 1971–1991 is shown in Fig. 1.



Figure 1. The age-dependent reproductive value (\mathbf{v} , right eigenvector of the average matrix) (open circles) and stable age distribution (\mathbf{u} , left eigenvector) of the red deer population (data from 1971–1991).

Analytical calculation of population growth rate in a variable environment

Calculation of exact population growth rates is analytically difficult in the stochastic case and has so far been possible only for a two-age class life-history (Tuljapurkar, 1990a). However, stochastic linearization has yielded an analytical approximation, for situations where the environmental variability is 'small' (Tuljapurkar, 1982).

$$a = \ln \lambda - \frac{\tau^2}{2\lambda^2} + \frac{\theta}{\lambda^2}$$

where a is the stochastic analogue of r , the population growth rate in a stochastic environment, $\ln \lambda = r$ from the Euler–Lotka equation, τ reflects the absolute amount of variation in the vital rates and also the pattern of covariation between them and ϕ reflects the correlation in environmental states between periods. If there is no correlation between periods (i.e. 'good' and 'bad' years occur at random) this term can be ignored, which considerably simplifies calculations.

Algorithms to calculate the small noise approximation of a were developed in MATHEMATICA (Wolfram Research Inc.) and FORTRAN77 computer languages, following the methodology described in Tuljapurkar (1982, 1990a). These are available on request.

Numerical approximation of population growth rate in a variable environment

In addition to the analytical approximation of a , a program to approximate a numerically was developed. This program simulated population growth in a density-independent environment. An initial population vector was specified (elements proportional to the stable age distribution) and then subjected to a sequence of 250 population projection matrices, chosen at random. For each stochastic population path, the per generation logarithmic rate of population growth is calculated. a can then be estimated numerically as the mean value of a distribution (i.e. E , the mathematical expectation) of many similar (in this case 1500) stochastic pathways (Tuljapurkar and Orzack, 1980):

$$a = \frac{1}{t} E(\ln N_t - \ln N_0)$$

where N_t is the population at time t and N_0 is the initial population size.

Elasticity and sensitivity analyses

We calculated the sensitivity of the population growth rate to changes in the matrix elements numerically, by varying each element of the mean matrix in turn (by addition of 0.001) and recalculating the population growth rate (r and Tuljapurkar's (1982) a). The sensitivity is simply the rate of change of fitness with change in the matrix elements (Caswell, 1989):

$$\frac{\partial r}{\partial m_{ij}} \text{ or } \frac{\partial a}{\partial m_{ij}}$$

However, as different life-history traits are liable to vary by different amounts (survivorships must vary between 0 and 1, fecundities may vary very differently), perhaps a more intuitive way to understand sensitivities is to calculate the change in fitness for a given proportional change in the matrix elements. This proportional sensitivity is known as the elasticity:

$$\frac{\partial r}{\partial m_{ij}} \frac{m_{ij}}{r} \text{ or } \frac{\partial a}{\partial m_{ij}} \frac{m_{ij}}{a}$$

(this can be thought of as the percentage change in r or a for a 1% change in m_{ij}).

The analytical formula for the sensitivity of λ to changes in the matrix elements is (Caswell 1989)

$$s_{ij} = \frac{v_i u_j}{\langle v, u \rangle}$$

where v_i is the i th element in the reproductive value eigenvector, u_j is j th element in the stable age distribution vector and $\langle . \rangle$ denotes the scalar product of the two vectors. The elasticity of r can be calculated as

$$e_{ij} = s_{ij} \frac{m_{ij}}{r}$$

To estimate the trade-offs between current fecundity, future fecundity and survivorships, the data for each age class were therefore separated into deer that had given birth (milk hinds) and deer that had not given birth (yeld hinds). It was therefore possible to investigate the costs of reproduction by comparing the survivorship of yeld and milk hinds and also the fecundity in the next year for milk and yeld hinds. For each of the relationships between: fecundity of milks, fecundity of yelds, survivorships of milks and survivorship of yelds versus age, a polynomial regression was fitted to the data. The survivorship cost of reproduction was calculated as the difference between the fitted values for yelds and milk hinds for each age class. The fecundity costs of reproduction were calculated as the difference between the fitted fecundity of milk and yeld hinds for each age. Using the calculated costs of reproduction and also the proportion of the females at any given age who were milk or yeld hinds it is possible to calculate the change in survivorship and fecundity in the next age class associated with a 1% change in current fecundity and also the change in current fecundity and fecundity in the next age class for a 1% change in current survivorship. Thus, for each element in the projection matrix we calculated the elasticity of fitness (r or a) assuming that for the current fecundity can be traded-off against current survivorship and future fecundity (i.e. the only way to increase fecundity is to decrease current survivorship and future fecundity and vice versa).

Testing the assumptions of the models

Stationarity. The techniques used here assume that the distribution of environmental states is constant (that is, there are no trends in the realization of environments through time). To test whether trends occur in the data, the autocorrelation functions were calculated for the following time series: annual rainfall, mean annual temperature, multiplicative increase in population size between years, adult mortality and female fecundity.

Constant matrix size. Until 1971–1972, the deer population on Rum was subject to annual culling, removing 17% of the annual spring count (Clutton-Brock and Albon, 1989). Cessation of culling allowed the population to grow for the first few years of the study (approximately 1971–1981) after which the population size fluctuated around a mean value. As a result of culling, the age distribution of hinds was curtailed for the early years of the study – many of the older animals had been shot. The mathematical techniques used in this study (both numerically and analytically) assume that the matrices remain a constant size from year to year (rather than, as in this case, growing as animals are permitted to survive to older age classes). To meet this requirement we replace the missing values of fecundity and survivorship in the early years with zeros. This has the effect of increasing the apparent environmental variance experienced by the population.

Results

The effect of environmental stochasticity on population growth rate in red deer

Variation in the deers' vital rates during the study. Considerable between-years' variation in the mean age-specific fecundity and survivorship is evident (Table 1). The amount of variation depends on which rate is considered, with an overall age-independent mean fecundity of 0.1512 ± 0.086 (coefficient of variation = 0.81) and an age-independent survivorship of 0.810 ± 0.19 (CV = 0.36). Correlations between variations in the different vital rates are generally quite weak, with the exception of correlations between the fecundities during the early part of adult life (age 3–14 years), which are strong and mostly significant (Table 2).

Testing the assumption of stationarity. Owing to the cessation of the cull at the start of the study, there are some *a priori* grounds for expecting non-stationarity in the environmental states throughout the study. For example, we might expect that the population released from culling would experience a strong trend towards decreased fertility and increased mortality as density dependence strengthens during the study. Although density-dependent changes in some vital rates have been noted (Clutton-Brock, *et al.*, 1982, 260; Clutton-Brock and Albon, 1989, Chapter 5), the relationship between density-dependent and -independent processes is not straightforward. For example, there are strong correlations between annual rainfall and adult mortality ($r = 0.549$, $p < 0.02$) and multiplicative change in population size and annual rainfall ($r = -0.695$,

Table 1. Mean fecundity and survivorship data for 1971–1991

Age (years)	Fecundity		Survivorship	
	Mean \pm SD	CV	Mean \pm SD	CV
1	0	0	0.902 ± 0.095	0.105
2	0	0	0.962 ± 0.041	0.042
3	0.086 ± 0.094	1.103	0.956 ± 0.063	0.066
4	0.202 ± 0.070	0.347	0.956 ± 0.054	0.057
5	0.241 ± 0.087	0.360	0.949 ± 0.065	0.068
6	0.209 ± 0.075	0.358	0.939 ± 0.083	0.089
7	0.212 ± 0.082	0.386	0.971 ± 0.062	0.064
8	0.215 ± 0.075	0.350	0.982 ± 0.060	0.061
9	0.219 ± 0.088	0.403	0.942 ± 0.073	0.078
10	0.225 ± 0.097	0.432	0.941 ± 0.118	0.125
11	0.206 ± 0.090	0.480	0.881 ± 0.122	0.139
12	0.231 ± 0.092	0.398	0.820 ± 0.195	0.238
13	0.249 ± 0.089	0.358	0.837 ± 0.232	0.278
14	0.190 ± 0.111	0.587	0.755 ± 0.346	0.458
15	0.142 ± 0.126	0.887	0.639 ± 0.424	0.664
16	0.082 ± 0.123	1.498	0.498 ± 0.443	0.889
17	0.062 ± 0.110	1.781	0.405 ± 0.490	1.210
18	0.078 ± 0.130	1.656	0.238 ± 0.436	1.833
19	0.025 ± 0.079	3.220		

Survivorships are survivorship from age class i to class $i + 1$. Fecundities are composed of two elements, the age-specific birth rate of female offspring (mean for all years = 0.27 ± 0.11) and the neonatal survivorship (from birth to 31 May the subsequent year, i.e. the next census: mean = 0.615 ± 0.147). For fecundities in particular, the coefficients of variation show that there is considerable year-to-year variation.

Table 2. The 1971–1991 correlation matrix of all age-specific vital rates, subdivided into the biologically meaningful age-classes of Brown *et al.* (1993)

	F ₃ –F ₄	F ₅ –F ₇	F ₈ –F ₁₂	F ₁₃ –F ₁₈	S ₁ –S ₂	S ₃ –S ₄	S ₅ –S ₇	S ₈ –S ₁₂	S ₁₃ –S ₁₈
F ₃ –F ₄	0.341 (1)								
F ₅ –F ₇	0.611±0.15 (6)	0.705±0.07 (5)							
F ₈ –F ₁₂	0.457±0.14 (10)	0.660±0.13 (15)	0.525±0.16 (10)						
F ₁₃ –F ₁₈	0.054±0.24 (14)	0.114±0.31 (21)	0.128±0.30 (35)	0.000±0.25 (7)					
S ₁ –S ₂	0.229±0.09 (4)	0.340±0.11 (6)	0.277±0.18 (10)	0.046±0.29 (2)	–0.131 (1)				
S ₃ –S ₄	0.068±0.23 (4)	0.053±0.36 (6)	0.059±0.32 (10)	–0.124±0.28 (14)	0.087±0.12 (2)	–0.099 (1)			
S ₅ –S ₇	0.167±0.11 (6)	0.162±0.17 (9)	0.110±0.23 (15)	–0.010±0.18 (21)	0.064±0.13 (6)	0.038±0.17 (6)	0.097±0.08 (3)		
S ₈ –S ₁₂	0.260±0.13 (10)	0.362±0.17 (15)	0.323±0.16 (25)	0.028±0.29 (35)	0.183±0.18 (10)	0.133±0.22 (1)	0.179±0.18 (15)	0.223±0.24 (1)	
S ₁₃ –S ₁₈	–0.105±0.24 (12)	–0.07 ±0.23 (18)	–0.024±0.24 (30)	0.060±0.27 (42)	0.075±0.23 (12)	–0.029±0.17 (2)	–0.068±0.26 (18)	0.047±0.26 (1)	0.020±0.32 (15)
									1

For each cell, the mean \pm SD correlation coefficients are given, along with the number of correlations in that cell (in brackets) and the number of these which are significant at $p \leq 0.05$. $\alpha_{19,0.05} = 0.43$. F_x and S_x refer to fecundity at age x and survivorship from age x to age x + 1. For example, there are six correlations between fecundities at ages 3 and 4 and fecundities at ages 5–7 (3 and 5, 6, 7 and 4 and 5, 6, 7), the average value of which is 0.611 ± 0.15 . Of these six correlations, five are significant at $p = 0.05$. Thus, a ‘good’ year for fecundity in ages 3 and 4 is also a ‘good’ year for fecundity in ages 5–7 (and vice versa).

$p < 0.001$) and annual rainfall and population size itself ($r = 0.474$, $p = 0.06$). It is likely that the processes of density-dependent and density-independent population regulation interact: higher densities mean more competition for food at important times, which makes animals more susceptible to a reduction in food brought about by stochastic variation in climate.

For the variables tested, all autocorrelation coefficients were insignificant (the critical value $(2/\sqrt{n})$; Diggle, 1990) = 0.436). The maximum coefficients were rainfall 0.333, lag 1; temperature –0.314, lag 3; mortality 0.390, lag 4; multiplicative increase 0.296, lag 4; and fertility –0.288, lag 5. Certain of the correlelograms indicated the presence of weak positive autocorrelation (Diggle, 1990), in particular those of rainfall, mortality and the multiplicative increase in population size from year to year (Fig. 2). These correlations appear to be strongest in the first half of the study, so below we calculate population growth rates for 1971–1981, 1982–1991 and for all years together.

Estimates of population growth rate. The estimations of the stochastic growth rate do not differ greatly from the calculation of the deterministic growth rate (Table 3). As expected, for all three analyses the estimate of the stochastic growth rate is lower than the deterministic growth rate.

Using Tuljapurkar’s (1982) ‘small noise’ approximation, the growth rates of the population in the stochastic environment are reduced by 1.8, 7.6 and 3.8% of the deterministic growth rates for 1971–1981, 1982–1991 and 1971–1991, respectively. The numerical approximation suggests that population growth rates are reduced by only 0.8, 1.6 and 0.6% for the three analyses. This difference between the approximations is unlikely to be due to rounding errors, but is more likely due to the distribution of the variations in the mean vital rates. The closeness between the methods of estimating the population growth rate has been shown to be sensitive to the

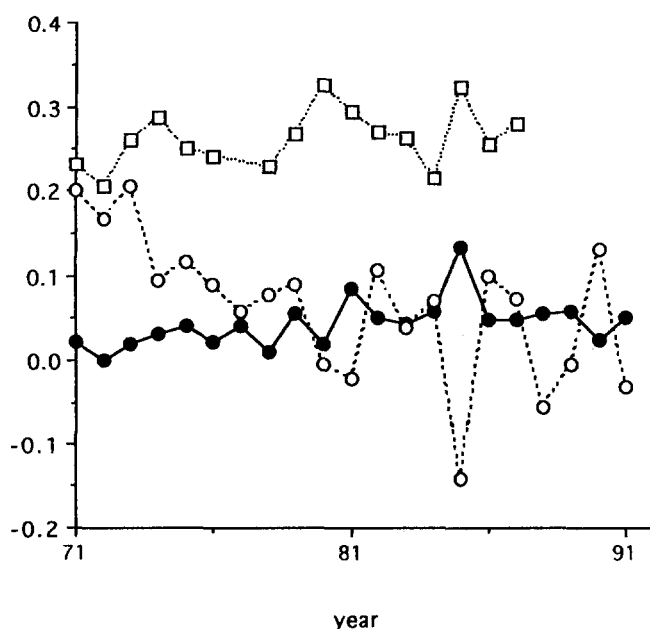


Figure 2. Time series of annual rainfall (01.06–31.05 each year) (squares), adult mortality (over same periods) (filled circles) and the multiplicative increase in population size from year to year (open circles). The correlation between adult mortality and rainfall = 0.549 ($p < 0.02$) and that between change in population size and rainfall = -0.695 ($p < 0.001$).

Table 3. Estimated population growth rates for the red deer in stochastic and deterministic environments

	1971–1981	1982–1991	1971–1991
r	0.09196	0.02162	0.05871
Tuljapurkar's (1982) a	0.09026	0.01997	0.05648
Difference ($a/r\%$)	0.00170 (98.2%)	0.00165 (92.4%)	0.00223 (96.2%)
Simulated r (\pm SD)	0.09192 ± 0.00331	0.02174 ± 0.00311	0.05874 ± 0.00379
Simulated a (\pm SD)	0.09123 ± 0.00331	0.02139 ± 0.00303	0.05837 ± 0.00378
(min – max)	(0.08091 – 0.10108)	(0.01127 – 0.03055)	(0.04397 – 0.06953)
Difference ($a/r\%$)	0.00069 (99.2%)	0.00035 (98.4%)	0.00062 (99.4%)
(min – max)	(-0.00094 – 0.00227)	(-0.00167 – 0.00232)	(-0.00170 – 0.00224)

r is the Malthusian parameter (annual per capita rate of population increase), which assumes a constant environment and a is the stochastic analogue of r . r and Tuljapurkar's (1982) a are calculated analytically (as the natural logarithm of the dominant eigenvalue of the mean projection matrix and from Tuljapurkar's (1982) small noise approximation, respectively). Simulated r and simulated a are calculated from 1500 independent bootstrap simulation runs, each of 250 'years' duration.

underlying distribution from which the variations in vital rates are chosen (Benton and Grant, in press) and, in many cases, the 'small noise' approximation overestimates the impact of stochastic variation on population growth rates.

The simulation study is instructive in that matrix multiplication is generally non-commutative so each independent 250 'year' stochastic realization of the environment will result in different rates of population growth. The distribution of these different growth rates is asymptotically log-

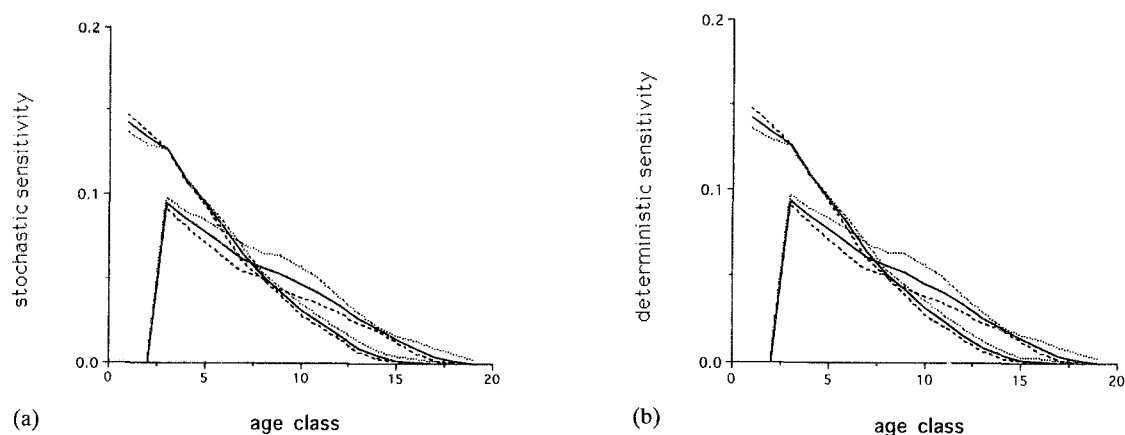


Figure 3. Sensitivities of (a) deterministic population growth rate (r) and (b) stochastic population growth rate (a) to changes in the survivorships (top three lines) and fecundities (lower three lines). Dashed lines 1971–1981, dotted lines 1982–1991 and solid lines 1971–1991.

normally distributed (Tuljapurkar and Orzack, 1980). The realized population growth rate can differ markedly from the expected (Table 3); the coefficient of variation for the estimates of stochastic growth rate varies from 3.6% (1971–1981) to 14.1% (1982–1991). For example, using the minimum and maximum values of the stochastic growth rate (from the 1971–1991 simulation) and assuming purely density-independent growth, would, starting with 100 animals, after 100 years produce final population sizes of 8120 and 104 628 (with a mean of 34 275) – a considerable range. So, although in general for these deer the stochastic environment does not have a large impact on the expected rate of population growth for any particular sequence of years the population size could fluctuate markedly.

Sensitivity and elasticity analyses

Sensitivity analysis estimates the change in the population growth rate caused by small changes in the matrix elements. The sensitivity of fitness to changes in the vital rates is equated with the selection pressures on those vital rates (Lande, 1982; Caswell, 1989): if fitness is not sensitive to changes in a life-history trait, then there will not be selection on genotypic variants of that trait. Conversely, if fitness changes markedly with variation in a trait, selection will be strong on genotypic variants of that trait.

In essence sensitivity analysis estimates the slope of the relationship between the fitness and magnitude of the vital rates. We can consider each vital rate as independent and ask the question ‘in which vital rates is fitness most sensitive to change?’. However, this is a somewhat abstract biological question as it is probable that changes in vital rates are not independent: trade-offs are likely to occur between them. Therefore, we first consider the sensitivity analysis in the absence of trade-offs and then incorporate the observed costs of reproduction to examine how trade-offs affect the selection pressures on the life-histories.

Sensitivity analysis with independently varying vital rates. The results of these sensitivity analyses for the three periods show little difference in the sensitivities between the deterministic and stochastic cases (Fig. 3a and b). The mean sensitivities of fecundities differ by 1.1, 1.4 and 1.6% for the three analyses of 1971–1981, 1982–1991 and 1971–1991, respectively and 0.2, 0.2 and 0.3%, respectively, for the survivorship sensitivities. We previously established that Tuljapurkar’s

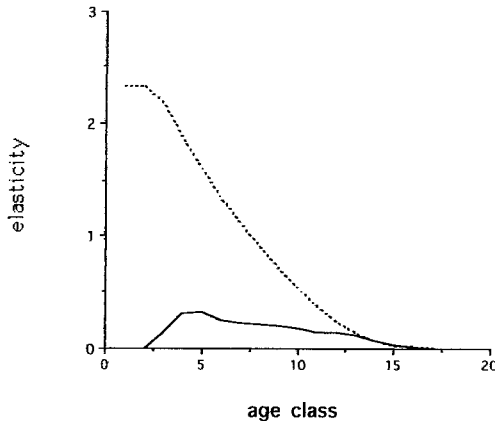


Figure 4. The deterministic elasticities (proportional change in fitness for a given proportional change in each vital rate) for the period 1971–1991. Dotted line, survivorship elasticities. Solid line, fecundity elasticities. Throughout most of their lives, a given increase in survivorship will cause a much greater increase in fitness than the same proportional change in fecundity, presumably because an increase in one year's fecundity has a 'one-off' benefit, whereas an increase in survivorship increases the mean reproductive success over subsequent years.

(1982) small noise approximation underestimates stochastic growth rate for these data. As the variance–co-variance matrix remains unchanging throughout the sensitivity analysis, it is probable that the stochastic growth rate is underestimated by a constant amount. If this is the case, the stochastic sensitivities will be unaffected by the approximation.

Elasticity is the proportional change in r resulting from a proportional change in the matrix elements (m_{ij}) (Fig. 4). As can be seen, up to the age of approximately 13 years, fitness is much more influenced by changes in survivorships rather than fecundities (a 1% change in early-year survivorships can increase r by nearly 2.4%, whereas a 1% change in fourth-year fecundity will only increase r by 0.35%).

Sensitivity analysis incorporating trade-offs. The above analyses look only at the rate of change of fitness with respect to the rate of change of each matrix element independently. It is extremely likely that changing one element results in the change of other elements due to trade-offs between current fecundity, future fecundity and survivorships. However, these analyses have a generality that is not given by incorporating trade-offs, because the costs of reproduction and, therefore the trade-offs, are likely to be highly dependent on the habitat and time at which the animals live. In the absence of these population- and time-specific costs, the general picture shows that fitness is much more sensitive to an increase in survivorships than an increase in fecundity.

For each age class, comparison of the survivorship and subsequent fecundity (i.e. in the following year) of yield (non-reproductive) and milk (reproductive) hinds allows the costs of reproduction to be estimated (Fig. 5). Using these costs we calculated the change in survivorship and subsequent fecundity associated with a 1% change in each age-specific fecundity and also the change in current and subsequent fecundity associated with a 1% change in each survivorship. These modifications were then used to calculate the change in fitness (elasticity) associated with changes in the life-history (Fig. 6). An increase in current fecundity is always selected for, even though it decreases both current survivorship and also fecundity in the next age class, whereas an increase in current survivorship is always strongly selected against, even though future fecundity is increased, because the current fecundity is decreased. There are essentially no differences

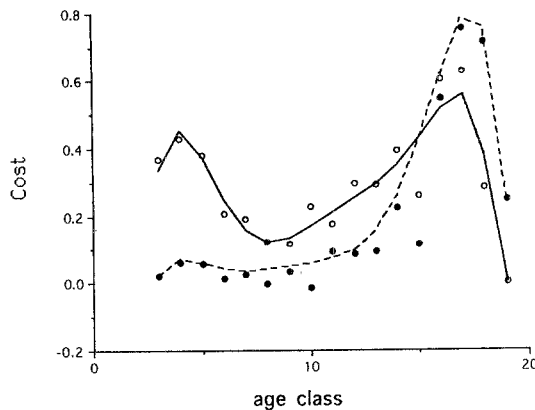


Figure 5. The age-specific costs of reproduction. These are the difference in fecundity at age $i + 1$ associated with having given birth (open circles) and the reduction in current survivorship associated with birth and suckling (closed circles). Polynomial regressions were fitted to the age-specific survivorships and fecundities of both milk and yield hinds. The difference between the fitted values, at each age, is the calculated cost of reproduction (fecundity cost, dashed line; survivorship cost, solid line).

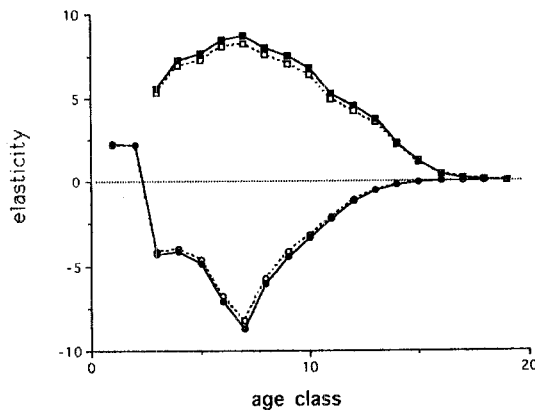


Figure 6. The elasticity of fitness calculated by incorporating the costs of reproduction (Fig. 5) into the analysis. Thus a 1% increase in survivorship at age 7 years causes a ~9% decrease in fitness, as to increase survivorship necessitates fewer females reproducing, even though future fecundity is increased. Squares, percent change in fitness associated with a 1% change in fecundity (multiplied by 50 so it fits on same scale). Circles, percent change in fitness associated with a 1% change in survivorships. Open symbols, elasticity calculated using deterministic techniques. Filled symbols, elasticity calculated using stochastic techniques. Mean values \pm SD are: fecundity elasticity – deterministic 0.087 ± 0.062 , stochastic 0.092 ± 0.065 ; survivorship elasticity – deterministic -2.265 ± 2.988 , stochastic -2.396 ± 3.146 .

between the elasticities calculated for r or a . It therefore seems that current fecundity is preferentially favoured by natural selection in either the deterministic or constant environment.

Thus, initially it seems that stochasticity does not influence the magnitude of fitness very much, nor the selection pressures on the life-history. However, it is likely that the shape of the trade-off functions may depend on the degree of environmental variance. For example, in a variable environment the costs of reproduction may be greater than in a constant environment. To investigate the effect of changing the costs of reproduction, two further elasticity analyses were conducted, the first incorporating a doubling of the currently observed costs and the second a

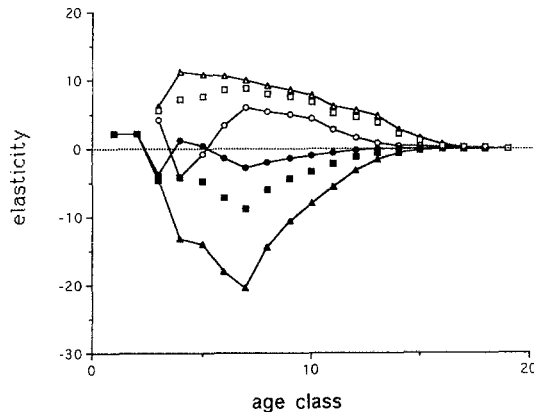


Figure 7. Changing the costs of reproduction changes elasticities. Open symbols, fecundity elasticities (calculated using stochastic methodology, multiplied by 50 to scale). Closed symbols, survivorship elasticities. Squares, observed costs of reproduction. Triangles, $0.5 \times$ observed costs. Circles, $2 \times$ observed costs. Decreasing the costs increases the benefit of fecundity over survivorship, such that survivorship is very strongly favoured to be traded-off against fecundity. Increasing the costs decreases the benefit of fecundity over survivorship, such that it may be profitable to trade-off fecundity in favour of increasing survivorship. Mean values \pm SD are fecundity elasticity observed costs 0.092 ± 0.065 , $2 \times$ costs 0.035 ± 0.054 , $0.5 \times$ costs 0.113 ± 0.082 , survivorship elasticity observed costs 2.396 ± 3.146 , $2 \times$ costs -0.412 ± 1.547 , $0.5 \times$ costs -6.110 ± 7.242 .

halving. As can be seen from Fig. 7, halving the costs causes the current fecundity to be even more strongly selected for and survivorships selected against, whereas doubling the costs causes increases in some fecundities to be selected against and increases in some survivorships to be selected for (if costs are increased further, e.g. by reducing fecundity in the next year to zero for milk hinds, all survivorships are selected for and all fecundities selected against). If an increase in survivorship can only occur through a decrease in the proportion of females giving birth (as assumed here) then cutting the costs decreases the difference in survival between milk and yield hinds and so increases the proportion of females having to be yield. The necessary reduction in fecundity associated with more females being yield, causes fitness to be reduced and so is strongly selected against. Conversely, doubling the costs increases the difference in survival between milk and yield hinds and thus decreases the proportion of females having to become yield to gain a mean increase in survivorship. For some age classes, the proportional reduction in milks, along with the increased cost in terms of future fecundity, is so great that an increase in survivorship is selected for.

So, although the deterministic and stochastic analyses give similar results in terms of fitness and selection pressures on life-history traits, it remains possible that evolutionary stochasticity influences the costs of reproduction and by doing so causes changes in the selection pressures on the animals' life-histories.

Discussion

The influence of climatic factors on the ecology of red deer on Rum is strong (Albon *et al.*, 1987; Albon and Clutton Brock, 1988; Albon *et al.*, 1992). The weather itself influences deer directly, such as through the increased costs of thermoregulation during severe weather, as well as indirectly by affecting the production of forage (the latter interacts with population density and determines the strength of density dependence). For example, the changes in population size each year correlates strongly with annual rainfall (as does both juvenile and adult mortality).

Population growth rates, calculated from year-specific projection matrices, differed markedly over the study ($\lambda = 1.0559 \pm 0.0751$, range 0.884–1.171), being more variable in later years indicating that at higher densities density-independent factors seem to have stronger effects. Given this considerable year-to-year variation in the life-histories of the red deer it is somewhat surprising that the difference this stochastic variation makes to the population and evolutionary biology at first sight appears so negligible. Using the small noise approximation of Tuljapurkar (1982) indicates that stochastic growth rates are reduced on average by $< 4\%$. Simulation methodology indicates Tuljapurkar's (1982) approximation overestimates the reduction in growth rates, instead estimating the reduction as $< 1\%$. Sensitivity analysis indicates that the selection pressures on the vital rates are very similar, differing by $\cong 1\%$. As a result, we conclude that, in the case of red deer, there is little difference in the results calculated using stochastic and deterministic techniques, thus allowing the considerable convenience of the use of standard methodology (Caswell, 1989).

The likely reason for stochastic independence in the red deer is that they have an extremely long, iteroparous, 'slow' (Read and Harvey, 1989) life-history already. If the deer were semelparous, then, following a disastrous year when fecundity was zero, a female would leave no descendants at all. Iteroparity allows for some lifetime reproductive success even if successful reproduction does not occur each year. Additionally, if some age classes are more prone to die in a 'bad' year, then by breeding throughout life, a female ensures that her offspring are not all in a susceptible age class simultaneously should a bad year occur during her lifetime. In effect, the life-history is buffered against large-scale environmental fluctuations because it is so long. A common response to environmental stochasticity is to increase the degree of iteroparity (Orzack and Tuljapurkar, 1989), which is already considerable in the case of the long-lived deer. The present life-history of these ungulates may therefore already be a response to environmental stochasticity. Inspection of Table 1 further reveals that the age classes most affected by environmentally induced stochasticity are the very young and the very old. The main age classes with a high reproductive value (Fig. 1) are relatively immune from environmental variation. Van Sickle (1990) conducted a simulation study from which he reached similar conclusions concerning the buffering effect of long life-histories.

Although the stochastic nature of the environment affects the mean population growth rates of the animals or the sensitivities *per se* little, it may not be true that environmental variation has little evolutionary impact on the life-history of these deer. Because the selection pressures on the life-histories are very sensitive to the trade-offs between life-history terms, changing the variability of the environment is likely to change the costs of reproduction (e.g. by increasing the mortality of pregnant over non-pregnant females) and thus change the selection pressures on the life-history.

The initial sensitivity analyses show that, in the absence of trade-offs between fecundity and survivorships, an increase in survivorships will be much more strongly selected for than a similar increase in fecundity, especially during the earlier part of life (Figs 3 and 4). This is a general result (Caswell, 1989). This is presumably due to the long-term benefits accruing by increasing current survivorship (increasing the chance of surviving to have some fecundity over many subsequent years), whereas increasing current fecundity has more of a one-off benefit. However, the picture changes radically when the observed costs of reproduction are incorporated into the analysis. Under current conditions, an increase in fecundity is selected for, even though it reduces both current survivorship and future fecundity. Conversely, an increase in current survivorship is selected against, even though it increases fecundity in the next year, because it reduces current fecundity. It should be noted that were the life-history 'optimal' the sensitivities/elasticities would be zero (the sensitivities measure the slope of the relationship between the magnitude of the vital rate and fitness: at the optimum fitness is maximized and the slope equals zero) (Caswell, 1989). This is almost the case for fecundities, but is a long way from the case for survivorships (Fig. 6)

where an increase in survivorship in favour of future fecundity is very strongly selected against. The non-optimal survivorships are perhaps the result of previous generations of hunting and culling over historical time and predation upon the old during evolutionary time. If, due to hunting and predation, the possibility of surviving to old age were small, middle-aged animals gained no benefit by delaying reproduction in favour of surviving to reproduce in the future – and so it was selected against. This appears maladaptive now predation has ceased. In support of the hypothesis, if the costs of reproduction are doubled (imagine predation on pregnant females and the very young), the survivorship elasticities tend more to zero (Fig. 7).

Changing the costs of reproduction changes the relative benefits of fecundity and survivorship (Fig. 7). The trade-off functions are likely to be very specific to the animals in their environment; changing the environment (e.g. by increasing the variance in stochastic events) is very likely to change the trade-offs and thereby select for different life-histories, even if the selection pressures estimated using stochastic and deterministic methods are similar. For example, increasing the costs of reproduction increases the benefit of trading off fecundity against survivorship.

The elasticity analysis suggests that, given the observed rates of survivorship and fecundity, females should always increase their fecundity even at the expense of survivorship and future fecundity. This raises the question of why many females do not breed each year, instead becoming yield hinds. The probability of conceiving in any one year is related both to female weight (there is a threshold female weight below which conception is unlikely, perhaps because below this threshold the costs of reproduction increase vastly) and also population density (the threshold is greater at higher densities) (Clutton-Brock and Albon, 1989). Thus, female fertility is determined by density-independent factors (the weather influencing food production) as well as density-dependent factors (competition for food) and these are likely to interact with female 'quality'. A high-quality, dominant female will be better at obtaining food, more likely to gain weight and, thus, conceive in any given year.

Differences in the sensitivities between the early years of the study and the later years of the study do exist (Fig. 3), most notably in the survivorships of very young animals (stronger selection to increase juvenile survivorship in the early years of the study) and the fecundities of adults (stronger selection to increase fecundities in later years of the study). The former effect may be an artefact created by the cessation of culling in 1972, in that in the early years of the study there were few animals surviving to old age. This would reduce the mean lifetime reproductive success, increasing the selection pressure to have more offspring surviving to adulthood. The increase in selection pressure on fecundities in later years of the study may be a response to more adults surviving to old age than in earlier years of the study. If the proportion of adults surviving is small, then any change in the fecundity of older females will have a small effect on fitness, whereas if there is a large proportion of adults surviving changes in their fecundity are going to make a larger impact on fitness.

Analytical calculation of stochastic growth rates is a considerable advantage in the investigation of the theoretical implications of non-deterministic environments (Tuljapurkar, 1990a); however, the assumptions needed to allow Tuljapurkar's (1982) small noise approximation to be accurate are quite stringent (Tuljapurkar, 1989; Grant and Benton, in press). The approximation works with 'small noises', that is, when the coefficients of variation are less than ~ 0.5 , though the approximation remains qualitatively correct at higher CVs (Tuljapurkar, 1989). In addition, the approximation considers only the means and variances of vital rates, whereas higher moments of the distribution of vital rates (e.g. its skewness) can have an appreciable influence on stochastic growth rate. Slade and Levenson (1984) showed that taking into account the observed positive skew for survivorship data in spruce budworm (rather just the means and variances) significantly increased estimates of the stochastic population growth rate. So although analytically useful, this approximation may not be particularly good for many organisms as the necessary conditions may not be fulfilled. For example, note, from Table 1, how the CVs are age dependent, as is the skew

of the distribution of variations. To find life-histories, particularly long ones, where the conditions are maintained throughout the life-history is perhaps unlikely. For students of stochastic demography, a combination of analytical and numerical techniques, as used here is perhaps sensible. However, with the simulation models, especially with long life-histories, care must be taken with verification to ensure the result is realistic (Ripley, 1987). Once, confirmed, however, simulation models can provide some degree of insight into stochastic population processes and at the present time they provide the best available approximation to the stochastic growth rate. We are currently undertaking an exhaustive examination of the accuracy of Tuljapurkar's (1982) approximation (Grant and Benton, in press).

The proper definition of fitness is one that has been considerably debated over many years (Charlesworth, 1980; Lande, 1982; Tuljapurkar, 1982; Metz *et al.*, 1992; Giske *et al.*, 1993; Kozłowski, 1993; Sibly and Curnow, 1993). Many behavioural ecologists content themselves with the use of the lifetime reproductive success (LRS) as the fitness measure to be used. However, as has been frequently discussed in the past, this is not always suitable for several reasons. First, it ignores the timing of reproduction in adult life (Giske *et al.* 1993). In a growing population, early reproduction will be generally favoured (just as placing money on deposit earlier gives greater gains if interest rates are positive) and in a shrinking population late reproduction will generally be favoured (just as placing money on deposit later reduces losses if one has to pay the bank to keep the money). Even in a constant population, if adult mortality is significant, early reproduction may be favoured because it reduces the risk of dying without reproducing (Sibly and Calow, 1986) (to extend the monetary analogy, if there is a chance of the money being stolen it is worth banking, even if you gain nothing else from the bank). Thus, the absolute number of offspring may become less important than the time at which they are born. Second, one cannot just consider the number of offspring, but also their survival and reproduction prospects and those of their offspring and so on. The growth rates of populations of genetically similar animals are often then used as fitness measures in environments where the assumptions necessary for the use of LRS are not met (growing, shrinking populations and so on). If the environment is strongly stochastic, Tuljapurkar (1982) identified, using a simple genetic model, a as the fitness measure to be used. For an empirical biologist, measures of reproductive success are the most straightforward to use and it is often safe to assume overall that the population is 'in equilibrium' (even if, within a patch, it is not) and ignore the complex measures of fitness (Kazwecki and Stearns, 1993). It may or may not be safe to assume that environmental stochasticity is unimportant in evolutionary terms, as the consequences of incorporating stochasticity into optimality models can vary the predicted optimum markedly (Orzack, 1985; Orzack and Tuljapurkar, 1989; Tuljapurkar, 1989; Benton and Grant, in press). However, in the case of the red deer on Rum, the population, since the early 1980s at least, is neither growing nor shrinking markedly and stochasticity *per se* is shown not to have much effect. In such a case, the mean LRS for females of a given genotype is the most suitable measure of fitness to use in evolutionary arguments (Clutton-Brock, 1988).

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