



Optimal Reproductive Effort in Stochastic, Density-Dependent Environments

Author(s): T. G. Benton and A. Grant

Source: *Evolution*, Vol. 53, No. 3 (Jun., 1999), pp. 677-688

Published by: Society for the Study of Evolution

Stable URL: <http://www.jstor.org/stable/2640709>

Accessed: 14-05-2017 11:31 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://about.jstor.org/terms>



Society for the Study of Evolution is collaborating with JSTOR to digitize, preserve and extend access to *Evolution*

OPTIMAL REPRODUCTIVE EFFORT IN STOCHASTIC, DENSITY-DEPENDENT ENVIRONMENTS

T. G. BENTON¹ AND A. GRANT²

¹Institute of Biological Sciences, University of Stirling, Stirling FK9 4LA, United Kingdom

E-mail: t.g.benton@stir.ac.uk

²School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom

E-mail: a.grant@uea.ac.uk

Abstract.—The amount of effort organisms should put into reproducing at any given time has been a matter of debate for many years. Early models suggested a simple rule of thumb: iteroparity should be favored when juvenile survival is relatively variable and semelparity when adult survival is relatively variable. When more mathematically complex models were developed, these simple conclusions were found to be special cases. Variability can select toward iteroparity or semelparity depending on a number of factors irrespective of relative adult/juvenile survival (e.g., the density-independent models of Orzack and Tuljapurkar). Using new techniques, we estimate the ESS reproductive effort for stage-structured models in density-dependent and stochastic conditions. We find that variability causes significant changes in reproductive effort, these changes are often small ($\pm 10\%$ of deterministic ESS effort, but up to 50% change in some instances), and the amount that effort increases or decreases depends on many factors (e.g., the deterministic population dynamics, the vital rates affected by density, the amount of variation, the correlations between the vital rates, the distribution from which the variation is drawn, and the deterministic ESS effort). In a variable environment, semelparity is the ESS in only 3.5% of cases; iteroparity is the rule.

Key words.—Density-dependence, iteroparity, reproductive effort, semelparity, stochastic environments.

Received March 27, 1998. Accepted January 25, 1999.

Historically, studies investigating the evolution of life-history strategies typically assumed that the organism's population size is unbounded and that the environment is constant. As a result of these assumptions, it is possible to use r , from the Euler-Lotka equation, as the definition of fitness. In a popular text book on life-history evolution, Stearns (1992, p. 33) comments: "The most widely used fitness measure is r . Predictions made with r have functioned well in both theory and experiment, but it may not work when environmental stochasticity, frequency dependence, or density dependence are important." Inspection of any population time-series will reveal that both the assumptions made to justify the use of r as a measure of fitness are invalid. Indefinitely unrestrained population growth is unknown, and the unrestrained decline of populations, leading to their extinction, is rare. Density dependence must therefore be a biological reality in all systems, at least occasionally. Additionally, time series will reveal fluctuations around the mean population size, which are most likely to result from stochastic environmental variation, although various density-dependent processes (such as delayed or overcompensating density dependence) can also cause variations in population sizes, even in a completely constant environment. Although there has long been a debate within population biology as to the relative effects of density-independent or density-dependent factors on populations, many investigations assume that populations are in equilibrium and that the environment is constant. As a result, in short-term adaptationist studies it is possible to use lifetime reproductive success (LRS, or R_0) as the definition of fitness (see examples in Clutton-Brock 1988). Studies assuming that the population is in equilibrium (when $\lambda = 1.0$, $r = 0$) are equivalent to studies assuming density independence with a stationary population. Populations in which $r = 0$ will become extinct almost surely due to demographic stochasticity (Renshaw 1991).

Therefore, the assumptions of environmental constancy and either lack of density-dependence or stationary, equilibrium populations are simplifying abstractions. Indeed, in a commonly used textbook on population biology, Begon et al. (1996, p. 180–181) state: "Although density-dependent processes are an absolute necessity as a means of regulating populations and are generally by no means unimportant in determining abundance, they may well be of only minor importance when it comes to explaining particular observed population sizes. Moreover, because all environments are variable . . . it is likely that *no* natural population is *ever* truly at equilibrium."

Thus, in attempting to make adaptive analyses tractable, unrealistic assumptions have typically been made. The effect of relaxing these assumptions has been a matter of some interest in recent years. Within life-history studies, a number of analyses have incorporated stochasticity within the density-independent scenarios. Such studies have commonly found that under conditions where stochasticity is marked, adaptive analyses produce quantitatively different predictions to the deterministic case. For example, variable environments (especially where juvenile mortality is more variable than adult mortality) may select for iteroparity in organisms, when otherwise semelparity would be selected: so-called bet-hedging (Murphy 1968; Schaffer 1974; Fox 1993). However, semelparity may also be favored 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 for mixed rather than pure strategies (Haccou and Iwasa 1995), for a mixture of pure strategies (Sasaki and Ellner 1995, 1997) or for a reduction in polymorphism (Van Dooren and Metz 1998). Variability may select for indeterminate growth rather than determinate growth (Gurney

and Middleton 1996) and may select phenotypic plasticity in some situations, but not others (Orzack 1985).

There is increasingly a consensus that adaptational analyses should be couched in terms of invasion dynamics (Metz et al. 1992; Rand et al. 1994; Ferriere and Gatto 1995; Mylius and Diekmann 1995; Gurney and Middleton 1996). To predict the outcome of selection one should model the invasion of a mutant into a population of residents. The "fittest" phenotype is the one that is unininvadable, rather than one that necessarily maximizes a quantity defined as "fitness." The invasion of a mutant phenotype into an established population is measured by a mathematical quantity, called the dominant Lyapunov exponent, linearized about the point where the population of the invader is zero. This quantity is termed the "invasion exponent" by Rand et al. (1994) and is symbolized by ϑ . In simple terms, if a mutant arises in an established population, ϑ is estimated as the growth rate of the invader population (the slope of the log-transformed, least-squares regression). Invasion can only occur if $\vartheta > 0$.

In this paper, we present the results of an investigation of life-history evolution in environments that are both stochastic and density dependent. To do this we assume a trade-off between current fecundity and survival in a number of different life histories. We find the unininvadable, ESS value of the proportional reproductive effort, E , for each life history in a number of different "environments" characterized by different types and amounts of stochasticity.

METHODS

We model the population dynamics using matrix population models (for a review, see Caswell (1989). The standard matrix model is:

$$\begin{pmatrix} F_1 & F_2 \\ S_1 & S_2 \end{pmatrix} \cdot \begin{pmatrix} n_{1(t)} \\ n_{2(t)} \end{pmatrix} = \begin{pmatrix} n_{1(t+1)} \\ n_{2(t+1)} \end{pmatrix}, \quad (1)$$

where the F_x represent the number of offspring born to an individual in age/stage class x and surviving until the next census. The S_x -values represent survival of an individual from age x to $x + 1$. Multiplication of the life-history matrix by the vector containing the numbers in each age/stage class (the $n_{x(t)}$) gives the numbers in each age class at the next time step.

This basic model is modified in three ways. First, we simulate the addition of stochastic variation in the vital rates (ϵ_x). Second, we assume that there is a trade-off between current fecundity and survival, measured by the proportional reproductive effort, E . We model this trade-off as a nonlinear function by multiplying the survivorship terms by $(1 - E^z)$, following Cooch and Ricklefs (1994). Third, we assume that some or all of the "realized" vital rates are some decreasing function of density ($f[\Delta]$, where $\Delta = n_1 + n_2$). Our model then becomes:

$$\begin{pmatrix} (F_1 \pm \epsilon_1) \cdot E \cdot f(\Delta), & (F_2 \pm \epsilon_2) \cdot E \cdot f(\Delta) \\ (S_1 \pm \epsilon_3) \cdot (1 - E^z) \cdot f(\Delta), & (S_2 \pm \epsilon_4) \cdot (1 - E^z) \cdot f(\Delta) \end{pmatrix} \cdot \begin{pmatrix} n_{1(t)} \\ n_{2(t)} \end{pmatrix} = \begin{pmatrix} n_{1(t+1)} \\ n_{2(t+1)} \end{pmatrix}. \quad (2)$$

Assessing the Impact of Stochasticity

To investigate the impact of stochasticity on the optimal life history, the following factors were varied. (1) The amount of variation (as measured by the coefficient of variation [CV] the ratio of the standard deviation to the mean). (2) The correlations between the variations in the vital rates. Sampling was conducted so that the rank correlations took the values 1, 0, or -1. This resulted in four patterns of variations, each pattern of variation can be described by three correlations: between fecundities, between survival terms, and between fecundities and survival. The four patterns are: (a) variations across all vital rates were positively correlated—a good year for one vital rate was also a good year for all others (correlations = 1, 1, 1); (b) variations across all vital rates were uncorrelated (correlations = 0, 0, 0); (c) variations between the fecundity terms and the survival terms were positively correlated, but between fecundities and survival there was a negative relationship—a good year for fecundities was a bad year for survival (correlations = 1, 1, -1); and (d) variations between the fecundities and survival were positively correlated, but there was no correlation between fecundities and survival (correlations = 1, 1, 0). (3) The sampling distribution from which the variations were drawn. Three basic patterns of variation were used. First, sampling for variations in fecundity was taken from a log-normal distribution and variations in survival were from a beta distribution. Second, we used a "mixed" distribution, whereby for each time period the value of the vital rate was taken as the mean \pm (CV \times mean). Whether the (CV \times mean) term was added or subtracted was decided independently for each time step. Such a "good-year" or "bad-year" scenario was used by Schaffer (1974). Sibly et al. (1991) showed that the predictions Schaffer made with such a distribution were robust to the choice of distribution. Third, we modelled a situation where organisms live in a constant environment, but one that is liable to periodic "catastrophic years." At a given average frequency, the matrix of vital rates was substituted with matrix with much reduced survival and/or fecundity terms. The time steps for each "catastrophe" were assigned randomly, to prevent any effects due to exact periodicity.

In all simulations, random deviates for each year were independent; we made no attempt to investigate the impact of serial autocorrelation.

Assessing the Impact of Density Dependence

The impact of density dependence on the optimal life history was investigated by varying the vital rates affected by density: either fecundity (which is the product of fertility and juvenile survival to the next census), survival, or both were density-dependent and by varying the function relating the vital rates to density: (1) Ricker density dependence: Each fecundity term is reduced by an amount given by $\exp(-\beta[N_{tot}])$, where β is a scaling constant and $N_{tot} = N_1 + N_2$ is the total population size; (2) Beverton and Holt density dependence: Each fecundity term is multiplied by $1/[1 + 2\beta(N_{tot})]$; (3) Usher density dependence, with gradual onset of density dependence: The density multiplier was given by $1/[1 + \exp(1.25\beta[N_{tot}] - 50,000\beta)]$; and (4) Usher density dependence, with sudden onset of density depen-

TABLE 1. The life histories (LH) used. The deterministic optimum effort is for $z = 6$. The parameters T_0 (generation time), R_0 (per capita reproductive success), and λ (population growth rate) are calculated for the mean matrix prior to the application of density dependence. F refers to environments where density affects fecundity terms only, S survivorship terms only, and F & S both together.

LH	Matrix elements				Deterministic ESS effort	T_0	R_0	λ	
	F ₁	F ₂	S ₁	S ₂					
1	0.1	2	0.8	0.95	F	0.463	3.72324	12.3745	1.45963
2	1.0	10.0	0.6	0.85	F	0.556	2.16102	19.0493	2.49475
					S	0.99	1.23194	1.3558	1.27395
3	0.5	5.0	0.5	0.75	F	0.556	2.46952	5.23446	1.68594
					F&S	0.69	2.29758	4.99493	1.75807
					S	0.747	2.2188	4.43075	1.74486
4	1.0	5.0	0.75	0.85	F	0.558	2.20526	12.1108	2.12193
					F&S	0.724	2.00235	9.25488	2.25025
					S	0.99	1.1695	1.21863	1.1819
5	4.0	10.0	0.6	0.85	F	0.565	1.461	20.7216	3.48962
					F&S	0.880	1.19507	8.71134	4.26273
6	1.0	4.0	0.5	0.75	F	0.614	2.09291	4.61903	1.74103
7	1.0	10.0	0.3	0.6	F	0.658	1.92385	4.70033	1.95248
					S	0.99	1.14074	1.17013	1.1464
8	0.85	15.0	0.1	0.5	F	0.695	1.85831	2.2534	1.48179
					F&S	0.748	1.7932	2.21089	1.49259
					S	0.847	1.6388	1.89052	1.43544
9	1.0	5.0	0.3	0.5	F	0.701	1.76368	2.35785	1.54226
					F&S	0.763	1.68721	2.29757	1.55756
					S	0.99	1.07973	1.07952	1.07324
10	4.0	10.0	0.3	0.6	F	0.703	1.21649	6.7369	3.45377
					F&S	0.981	1.02061	4.26629	4.00521
11	1.0	10.0	0.3	0.3	F	0.720	1.71385	3.2262	1.872
					S	0.99	1.13691	1.16691	1.14426
12	1.0	10.0	0.1	0.3	F	0.765	1.51715	1.56969	1.32743
					S	0.99	1.05474	1.04897	1.04632
13	4.0	10.0	0.3	0.3	F	0.785	1.15286	5.48215	3.66511
					F&S	0.984	1.01722	4.21604	4.00447
14	4.0	10.0	0.1	0.3	F	0.910	1.03002	4.09181	3.74866
					F&S	1.000	1.000	4.000	4.000
15	5.0	2.5	0.5	0.3	F	0.912	1.02349	5.1147	4.66664

dence: The density multiplier was $1/[1 + \exp(12.5\beta[N_{tot}] - 500,000\beta)]$.

The parameters chosen were such that the equilibrium population size under each type of density dependence was similar (within 10%). β took the value of 2×10^{-5} throughout. For most life histories and most values of reproductive effort, the Usher-sudden-onset density dependence (4) made the underlying deterministic population dynamics chaotic. The vast majority of other combinations of density dependence, life history, and E resulted in equilibrium dynamics, although a few examples of bifurcations to limit cycles were encountered with large values of E .

We investigated the impact of stochasticity and density dependence on 15 life histories (Table 1). The basic matrices (without the trade-off and without the impact of density) varied from those with low fecundity and high survival to those with high fecundity and low survival. With the addition of density and the trade-off, this represents a range of ESS life histories from completely semelparous (matrix of $\{ \{4, 0\}, \{0, 0\} \}$) to markedly iteroparous (matrix of $\{ \{0.05, 0.93\}, \{0.79, 0.94\} \}$).

The ESS value of the proportional reproductive effort was identified using the elasticity method of Grant (1997), based on the mathematics of invasion developed in recent years (Metz et al. 1992; Rand et al. 1994; Ferriere and Gatto 1995). Rand et al. (1994) identify a parameter, ϑ , the invasion exponent, which can be used to find the evolutionarily stable

attractor (ESA) in a dynamical system, whatever the underlying dynamics. ϑ is equivalent to the dominant Lyapunov exponent of the system, as discussed by Tuljapurkar (1989), Metz et al. (1992), and Ferriere and Gatto (1995). Grant (1997) suggested a method of estimating the elasticity of vital rates. We here apply this technique to estimating the optimal value of the effort. The technique involves numerical differentiation of ϑ with respect to E . In short, a population of residents is modeled using equation (2) until the population dynamics have stabilized on the attractor (whatever its underlying dynamics). An invader population with the same life history as the resident, but with E very slightly different (here we use $0.995E$), is then simulated, starting with a small population and ignoring demographic stochasticity. The invader population does not contribute to the density dependence, thus linearizing the system about the point where the invading population is zero. The sign of ϑ then measures whether the invader manages to invade, and the magnitude of the partial differential ($\delta\vartheta/\delta\log E$) is a measure of the sensitivity of ϑ to change in E , and thus a measure of the selection pressure on E . The ESA for E is given by the condition $\delta\vartheta/\delta\log E = 0$. An example analysis is shown in Figure 1A, where the elasticity of ϑ to change in E is evaluated for E ranging from zero to one. Confirmation that the case when the elasticity equals zero is in fact the ESA is shown in Figure 1B: All other possible values of E have elasticity (and thus ϑ) less than zero and thus do not invade. It is possible (although

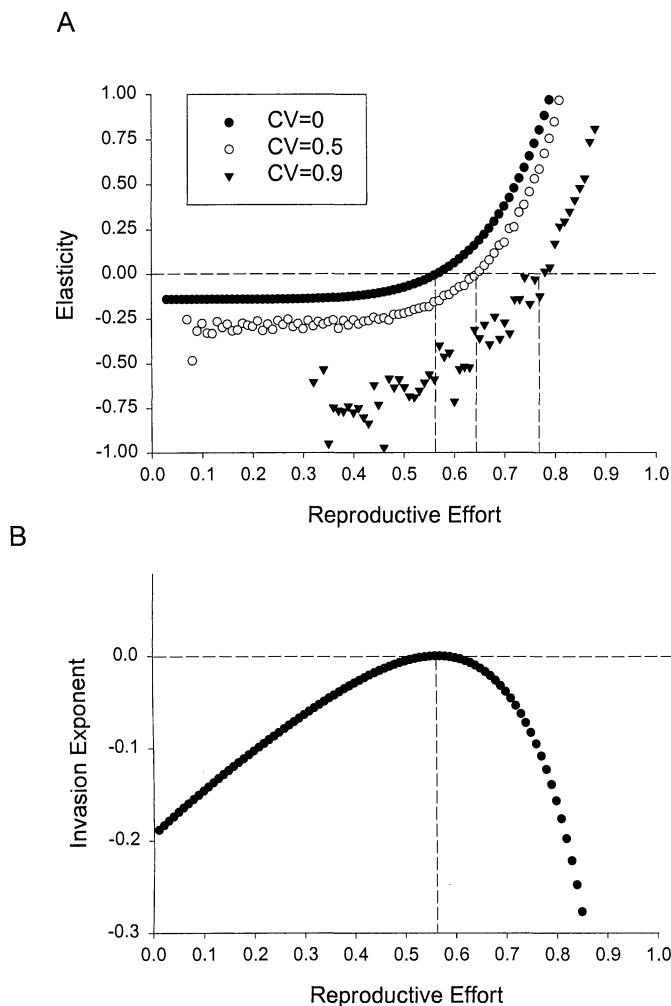


FIG. 1. Estimating ESS effort. (A) The elasticity of the invasion exponent with respect to change in effort ($\delta\vartheta/\delta\log E$) is plotted against E , where elasticity = 0 is the optimal, unininvadable, strategy. Open circles, deterministic environment (ESS effort = 0.565); closed circles, stochastic environment, $CV = 0.5$ (ESS = 0.645); squares, stochastic environment, $CV = 0.9$ (ESS = 0.76). For noisy data, such as $CV = 0.9$, elasticity = 0 was determined by regression methods. Life history 5 (see Table 1) using mixed distribution, Ricker density dependence. (B) Confirmation that the deterministic ESS = 0.565. The resident population is set at $E = 0.565$, all values of $E = 0.565$ have $\vartheta < 0$, that is, $E = 0.565$ is an evolutionarily stable attractor: It is unininvadable by any other value of E . ($\vartheta = -0.00002$ for $E = 0.56$, $\vartheta = -0.00005$ for $E = 0.57$).

rare) for there to be multiple (local) ESAs. When this occurs, the mutual invasibility of each local ESA can be tested to find whether they stably coexist or whether one invades the others and can be considered the global ESA. Throughout, we refer to the ESA value of effort as the ESS effort.

Procedures were written in Fortran 77 to estimate ϑ . Computationally, ϑ is measured as the growth rate of the invader population in an environment dominated by the residents (the numbers of which cause the density dependence). The average slope of the least-squares regression of the logarithm of invader population size on time estimates the invader population's growth rate (Rand et al. 1994; Grant 1997). Invasion attempts were of length 50 time-steps for most simulations,

but 100 for the ones simulating catastrophic events. Each value of ϑ was calculated from 1000 independent replicate invasion attempts, or 500 in the case of catastrophes. The ESS value of effort, where $\delta\vartheta/\delta\log E = 0$, was estimated in a number of ways, depending on the scatter in the relationship between E and $\delta\vartheta/\delta\log E$. When scatter is low, the value can be calculated by interpolation. In most situations, $\delta\vartheta/\delta\log E = 0$ was read directly off a graph. In cases where scatter is high, polynomial regression was used. The precision of these methods was estimated using the same life history, at medium variation ($CV = 0.5$) and high variation ($CV = 0.9$), with density dependence following the four different functions outlined above. $\delta\vartheta/\delta\log E = 0$ was estimated 10 times independently for each combination of CV and density dependence. The repeatability (intraclass correlation coefficient; Lessells and Boag 1987) was 0.9988 for medium variation, 0.9536 for high variation, and 0.9925 when combining the analyses. Therefore, the precision of the estimate of ESS effort declines with increasing variation, but can nonetheless be estimated with some confidence.

Simulations were conducted on the University of Stirling's HP9000/887 computer. Random deviates were selected using routines from the NAG library. Copies of the programs are available from the authors on request.

RESULTS

The Shape of the Trade-Off Influences How a Life History Responds to Variation

The shape of the trade-off between current survival and reproduction is determined by the exponent z . Using a set of four life histories (Table 1: 5, 10, 13 and 14) and varying both z and the CV shows that both have a marked effect on ESS value of reproductive effort (Fig. 2; GLM; z : $F_{1,90} = 32.08$, $P < 0.0005$; z^2 : $F_{1,90} = 23.52$, $P < 0.0005$; CV : $F_{1,90} = 14.12$, $P < 0.0005$, $CV * z$: $F_{1,90} = 13.24$, $P < 0.0005$; $CV * z^2$: $F_{1,90} = 7.54$, $P = 0.007$). In life histories tending toward semelparity, the ESS effort is 1.0 for low values of z and remains high (0.9–1.0) for higher values of z . In such life histories, variation tends to reduce the ESS effort and leads to similar ESSs irrespective of the value of z (Fig. 2A). Conversely, in more iteroparous life histories, increasing z initially reduces the ESS effort, but thereafter an increase in z causes an increase in ESS effort (Fig. 2D). In these cases, variation increases ESS effort; again, in relatively variable environments, the ESS efforts vary little, irrespective of the value of z . In general, the biggest change in ESS effort caused by variability occurs when z is low (i.e., the trade-off is more linear). Ricklefs (1977) found in populations of lowland birds that $z = 6$ was close to the mean value. We thus take this value in investigating the impact of other factors.

The Influence of Having Separate Trade-Offs on ESS Effort

In investigating the impact of other factors on the ESS effort, we assume that there is one age-independent effort that is optimized. The effects of relaxing this assumption are shown in Figure 3, where the effort for the first age class is fixed at different values and the ESS found for the other age class. In deterministic conditions, or where variation is small

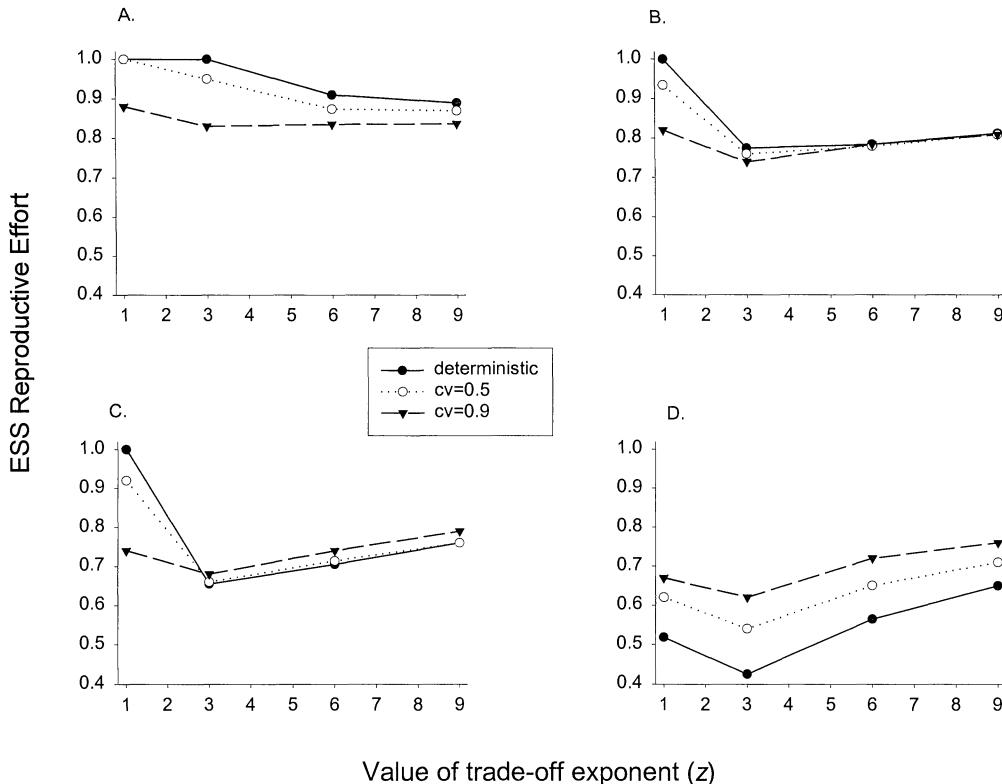


FIG. 2. The ESS effort plotted against the value of the trade-off exponent, z , for different amounts of variation (0, CV = 0.5 or 0.9). (A) Life history 14; (B) life history 13; (C) life history 10; (D) life history 5. Lower values of z generally produced greater changes in optimum effort for a given CV.

(Fig. 3A,D), the ESS value of the second age class's trade-off is generally little affected by the value of the first age class's effort. Variation also has a greater impact the lower the value of the fixed first trade-off, and causes an increase in ESS effort. The exceptions to these generalities (Fig. 3B,C, at low values of E_1) are associated with underlying nonlinear dynamics. For example, with the life history in Figure 3B the underlying dynamics are two-cycles with $E_1 = 0.25$ and $E_2 > 0.78$; whereas with $E_1 = 0.5$ the underlying dynamics are two cycles only when $E_2 > 0.95$. The ESS efforts are 1.0 and 0.88, respectively. With the addition of noise, the two cycles are obliterated and the dynamics of the two cases are much more similar than in the deterministic case, resulting in ESS efforts of 0.94 and 0.92, respectively.

The Effect of Only Fecundities or Only Survivorships Varying

In investigating the impact of other factors we assume that both fecundities and survival vary similar amounts at the same time. The effects of varying only fecundities or only survival are illustrated in Figure 4. As can be seen, the impact of variation depends on which vital rates are density dependent. If density dependence does not act on one part of the life history (such as on fecundities), then density-independent variation in those vital rates has a disproportionate effect, because without density-independent influences they would otherwise be constant. Conversely, if density dependence already acts on those vital rates, then the optimal effort will

have already evolved to compensate for the vital rates varying due to changing densities, and so the addition of density-independent variation has a smaller impact.

Having ascertained the impact of varying z , assuming a single trade-off and varying only fecundities or survival, nearly 700 simulations were conducted with the conservative estimate of $z = 6$ (Ricklefs 1977), one trade-off (thus only one reproductive effort to optimize), and with variability affecting both survival and fecundities. The quantitative results given below, in combination with those above, can allow qualitative extrapolation to situations where, for example, $z = 6$. The results of an analysis of variance for these data is given in Table 2.

Owing to the unbalanced design, significance tests could not be carried out on all interaction terms, but the analysis includes all the pairwise interactions that are significant. The adjusted R^2 for the model is 83.5%, with 41% accounted for by factors relating to variability (such as the CV, the correlations, the type of sampling distribution) and their interactions.

The Effect of Variation on the ESS Effort

The amount of variation (measured by the CV, ratio of standard deviation to the mean) has a highly significant impact on the ESS life history in a given "environment" (a covariate in the GLM of Table 2). The greater the variability, the greater the possible change in the optimal effort (Fig. 5): At CVs greater than about 0.5, the ESS Effort may be 75–

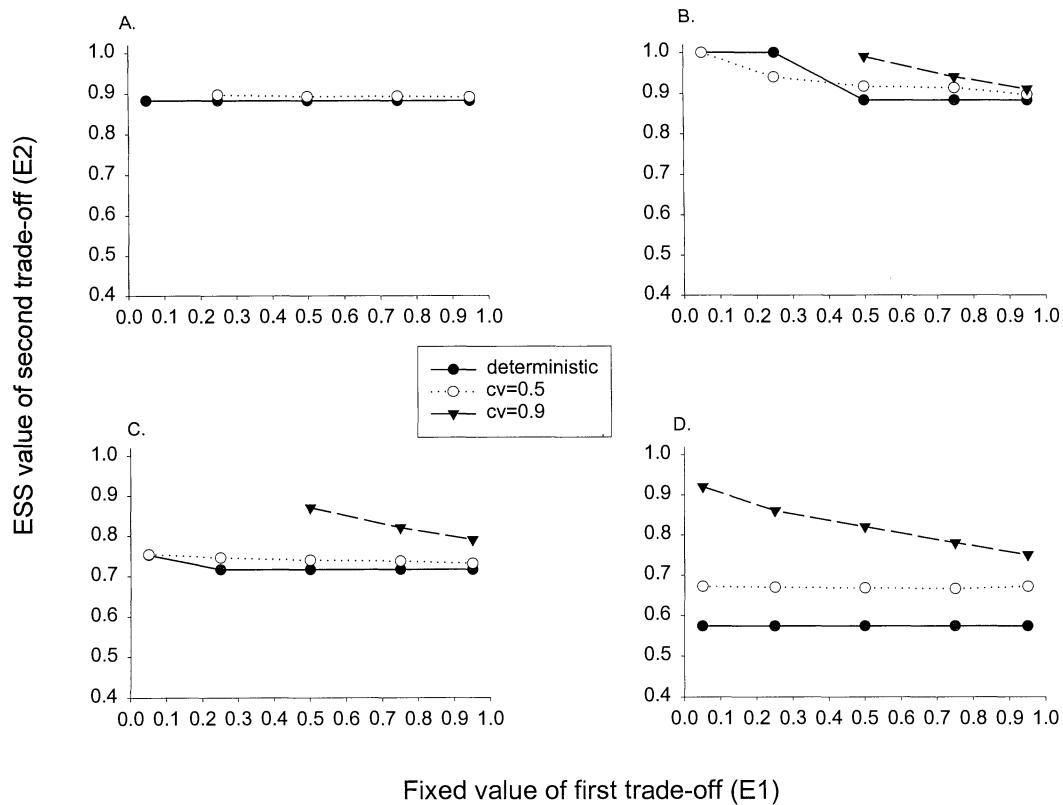


FIG. 3. The relationship between a fixed first-age-class effort and the ESS value of the second-age-class effort under different amounts of variation. (A) Life history 14; (B) life history 13; (C) life history 10; (D) life history 5. Fixing one effort generally has a small impact on the ESS second effort.

140% of the deterministic ESS. The greatest change in the optimum occurs in the most variable environments. However, variability interacts with many other factors, so that living in a variable environment does not necessarily mean that the

stochastic ESS effort will be markedly different from the deterministic effort (which remains the strongest predictor of stochastic effort; Table 2). For similar amounts of variability ($CV \approx 0.6\text{--}0.9$), the average change in ESS effort was 0.09 ± 0.07 (range = $-0.23\text{--}0.25$, median = 0.08, $n = 297$), which represents an average change of $12 \pm 10\%$ (range = $-23\text{--}49\%$).

A notable reason that high CVs do not have uniformly large effects is the interaction between the deterministic optimum and the stochastic optimum, as illustrated in Figure 6. The greatest changes in the optimum occur when the deterministic optimum is at the extremes of those investigated: Very iteroparous life histories become more semelparous and very semelparous life histories become more iteroparous, whereas those in between change least (coefficients from GLM in Table 2: $CV = 0.565$, $CV * \text{deterministic optimum} = -0.722$). This is also illustrated in Figure 2, where variability decreases ESS effort in the most semelparous life history (Fig. 2A), but increases it in the most iteroparous (Fig. 2D), while changing it little in intermediate life histories (Fig. 2B,C).

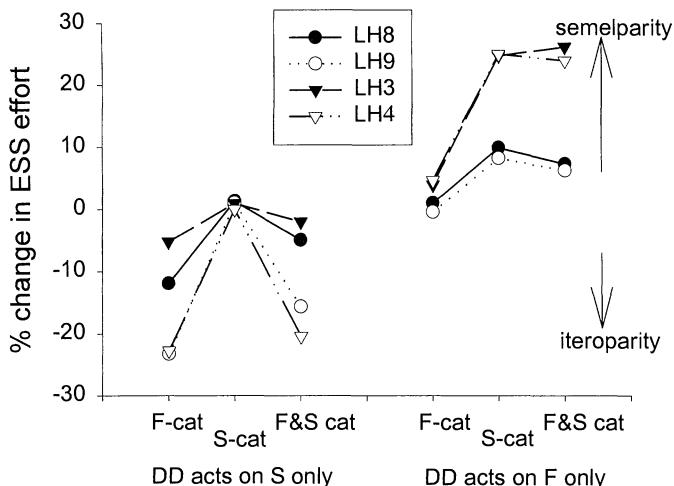


FIG. 4. The effect of varying only fecundities (F) or only survivorships (S) when survival or fecundities are density dependent (DD). The sampling distribution is "catastrophe," with vital rates being set to 0.01 every five generations, on average. The y-axis is the percentage difference between stochastic and deterministic ESS efforts. The four life histories are 3, 4, 8, and 9 (Table 1).

The Influence of the Vital Rates Affected by Density Dependence

Whether stochasticity increases or decreases the ESS effort (and by how much) is strongly influenced by the vital rates on which density dependence acts (Fig. 7). This is partly

TABLE 2. Results of ANOVA with the response variable being the ESS effort in stochastic environment and the predictor variables being: det ESS, ESS effort in constant environment; CV, coefficient of variation; corr, correlations between vital rates; DP, vital rates affected by density; SD, sampling distribution; DD, model of density dependence. Pairwise interactions not significant (and so removed from model) were: DD*corr, DD*SD, Corr*SD. Unbalanced design meant tests of the following pairwise interactions were not possible: corr*DP, SD*DP.

Source	df	F	P	R^2
det ESS	1	1472.13	0.000	40.0
CV	1	260.54	0.000	7.1
corr	7	21.32	0.000	4.0
DP	2	40.47	0.000	2.2
SD	2	7.23	0.001	0.4
DD	3	4.00	0.008	0.3
CV*corr	7	60.74	0.000	11.6
CV*det ESS	1	322.62	0.000	8.8
CV*DP	2	10.13	0.000	5.5
det ESS*DP	2	60.13	0.000	3.3
det ESS*corr	7	16.81	0.000	3.2
DD*DP	6	8.16	0.000	1.3
det ESS*SD	2	6.89	0.001	0.4
det ESS*DD	3	3.60	0.013	0.3
Error	607			
Total	653			83.5

because the deterministic ESS effort is strongly affected by which vital rates are density dependent. If survival alone is density dependent, the deterministic optimum effort tends toward one (median = 0.99, interquartile range = 0.990–0.999, range = 0.75–1.0, $n = 21$). If fecundity alone is density dependent, the deterministic optimum tends to be much lower (median = 0.702, interquartile range = 0.565–0.785, range = 0.463–0.912). If both fecundity and survival are density dependent, the deterministic optimum is between the two (median = 0.984, interquartile range = 0.88–1.0; range = 0.69–1.0). The difference between the deterministic ESSs

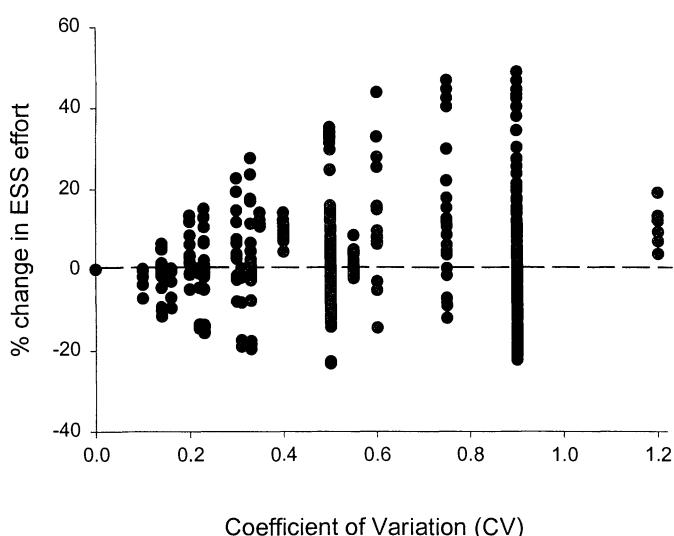


FIG. 5. The relationship between percentage change in ESS effort and the amount of variation (measured as the CV). $N = 685$ measurements of 15 different life histories in range of environments, with differing correlations, sampling distributions, density-dependent functions, and correlations between vital rates.

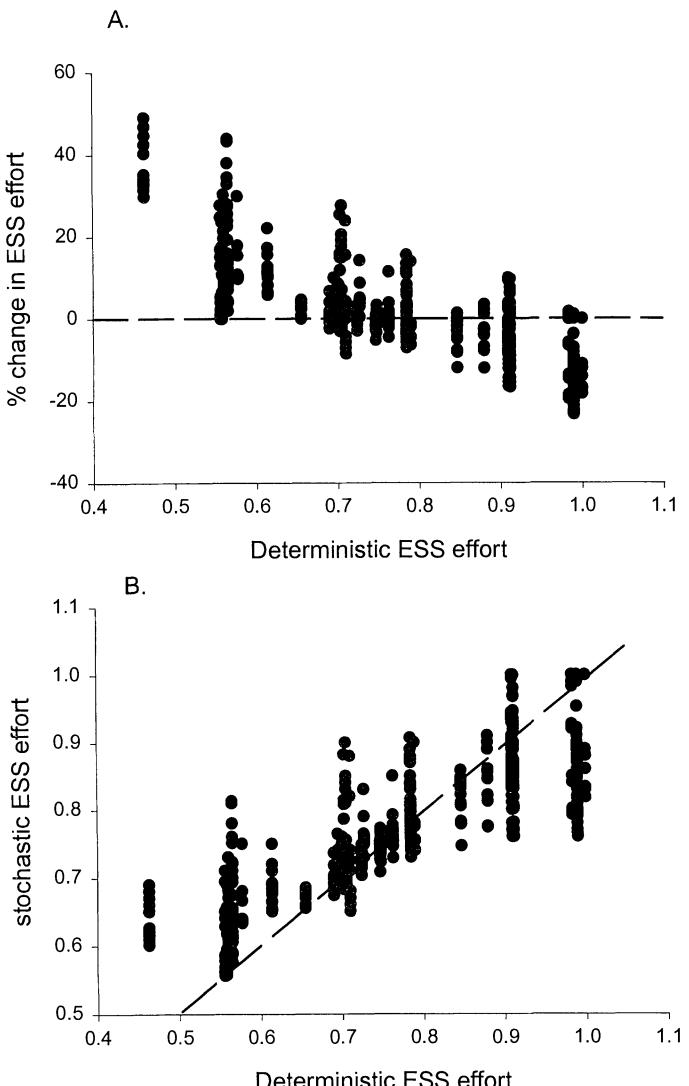


FIG. 6. The direction of and magnitude of change in ESS effort is strongly influenced by the deterministic ESS. Life histories with a low deterministic ESS become markedly less iteroparous. Those with high deterministic ESS become more iteroparous. (A) Change in ESS effort plotted against deterministic ESS effort (dashed line is $y = 0$); (B) stochastic ESS effort plotted against deterministic ESS effort (dashed line is $y = x$).

when density dependence acts on survival alone, fecundities alone, or both is highly significant (GLM, on square-root-transformed data, blocking by different life histories and density-dependence function: $F_{2,60} = 97.1$, $P < 0.0005$). As a result of the deterministic optimum approaching one if survival is density dependent, the most likely impact of environmental variability will be to reduce the optimal effort (making the life history more iteroparous). With density-dependent fecundity and a deterministic ESS effort of ~0.7, environmental variability has scope to reduce or increase the effort (Fig. 7). Does the fact that the deterministic ESS effort is close to one when survival is density dependent explain the fact that stochasticity tends to reduce the ESS effort in these cases? For two life histories (Table 1: 3 and 8) when survival is density dependent the deterministic ESSs are

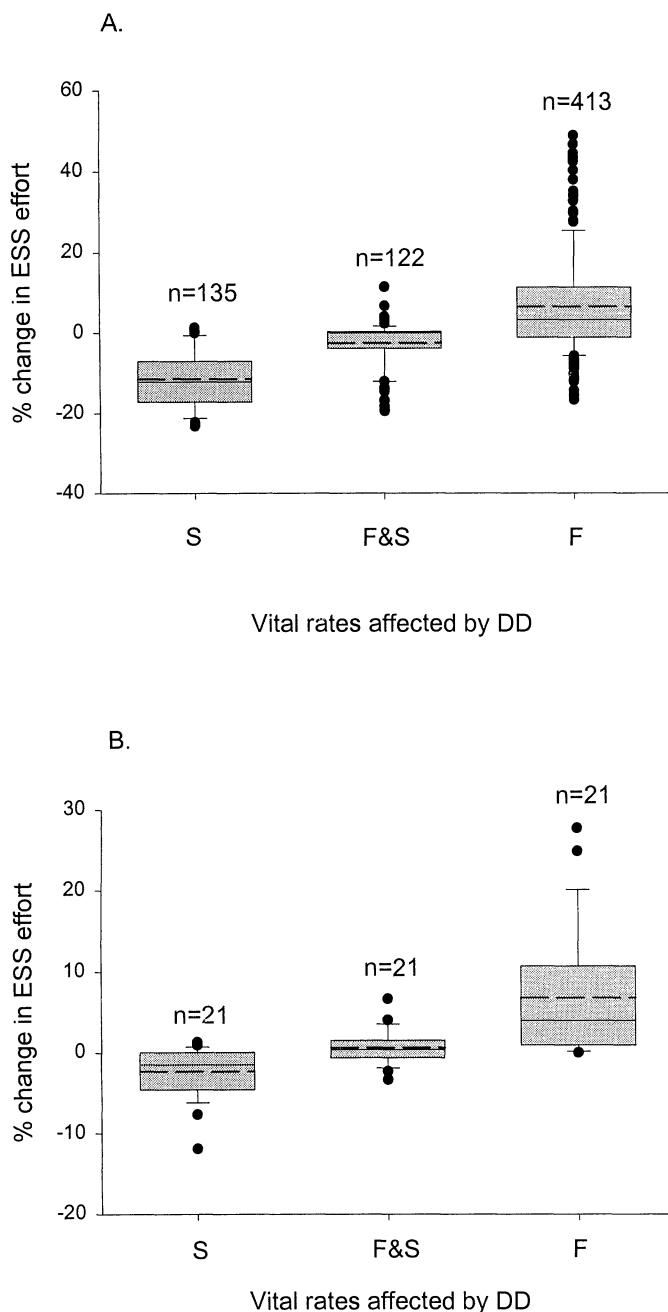


FIG. 7. The change in ESS effort varies with the vital rates affected by density dependence. (A) using whole dataset; (B) using a subset of two life histories (3 and 8), whose deterministic optima when density dependence (DD) acts on survivorships is less than 0.99. Box plots: box gives the interquartile range, median is solid line, mean is dashed line, whiskers give 10th and 90th percentiles, outliers are shown as solid dots.

much lower than one (0.75 and 0.85, respectively), so it is possible to look at the impact of variation on the life history and its interaction with the vital rates affected by density dependence. In these cases, variation still tends to reduce the optimum effort when survival is density dependent (Fig. 7b), whereas variation still tends to increase the optimum when fecundity is density dependent.

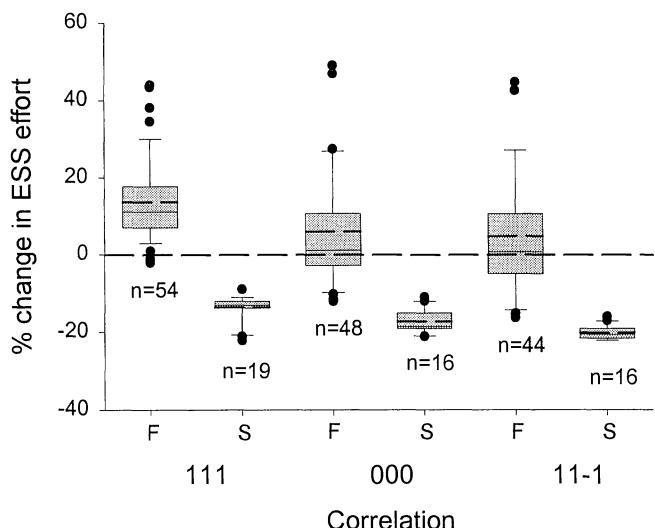


FIG. 8. The change in ESS effort depends both on the correlation between vital rates and the vital rates affected by density dependence. Subset of data where CVs > 0.6. F, density-dependent fecundities; S, density-dependent survival; 111, correlations are strong and positive; 000, all vital rates vary independently; 11-1, fecundities and survivorships covary negatively. The three correlations differ significantly for F and S ($H_2 = 21.2$ and 20.1, respectively, $P < 0.0005$). Box plots: box gives the interquartile range, median is solid lines, mean is dashed line, whiskers give 10th and 90th percentiles, outliers are shown as solid dots.

The Influence of the Correlations between Variations in Vital Rates

The way that variations in the vital rates are correlated has a significant influence on the optimal effort (Table 2). This impact interacts with the vital rates on which density dependence acts (Fig. 8), presumably for reasons similar to those outlined above. When there is strong positive correlation between variations in the vital rates (a good year for fecundities is a good year for survival) and fecundity is density dependent, there is, on average, a substantial increase in optimum effort (i.e., variability causes life histories to become more semelparous). Conversely, when survival is density dependent, variability tends to cause a slight decrease in optimum effort (i.e., toward iteroparity). When there is a strong negative correlation between fecundities and survival (a good year for fecundities is a bad year for survival), variation can cause an increase or decrease in effort when fecundity is density dependent, but it causes a very large decrease in effort when survival is density dependent. When all vital rates vary independently and fecundity is density dependent, again, variation can act to increase or decrease the optimum effort; but when survival is density dependent, variation causes a substantial decrease in effort (Fig. 8).

The Influence of the Sampling Distribution

Three classes of sampling distribution were used: continuous variation (log-normal distribution of fecundities, beta distribution for survival) and discontinuous variation (a symmetrical "mixed" distribution of "good" vs. "bad" years around a mean and an asymmetrical distribution where occasional "catastrophes" reduced the vital rates, with an oth-

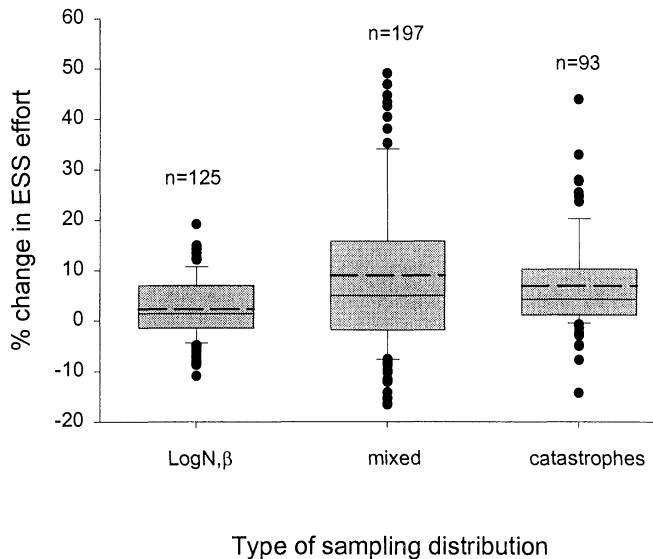


FIG. 9. Variation sampled from different distributions has different effects—continuous distributions create less variability in the change in ESS effort than “mixed” or “catastrophic.” Additionally, the location of the median differs between the sampling distributions. LogN,β, log-normal variation in fecundities, beta distribution for survivorships. Mixed, each year is either good or bad. Catastrophic, occasional years when vital rates set to low level (usually 0.1 or 0.01). Box plots: box gives the interquartile range, median is solid line, mean is dashed line, whiskers give 10th and 90th percentiles, outliers are shown as solid dots.

erwise constant mean value). The sampling distribution from which variation was drawn has a significant impact on the optimum effort (Fig. 9, Table 2). The most notable effect is that the discontinuous distributions tend to cause greater changes in life histories under similar conditions (Fig. 9; Levene's homogeneity test = 36.7, $P < 0.0005$).

Under the regime of catastrophic events, catastrophes could either affect fecundities or survival. When fecundity is density dependent, the impact of catastrophic reductions on survival is much greater (causing increase in effort toward semelparity) than catastrophic reductions in fecundities (which may increase effort when optimum is low or decrease it when optimum is high; Fig. 4). Conversely, when survival is density dependent, the impact of occasional catastrophic reductions in survival is slight, but the impact of occasional catastrophic reductions in fecundities is large (and negative, thus selecting greater iteroparity).

The Influence of the Type of Density Dependence

There is an influence of the density-dependent function used to generate the population regulation (Table 2). There is also an interaction between the density dependence and the deterministic optimum, due to the deterministic optimum differing depending on the function used and so the underlying dynamics (Van Dooren and Metz 1998). The coefficients from the model of Table 2 (not shown), indicate that much (although not all) of this effect is between Usher-strong density dependence and the others (Ricker, Beverton and Holt, Usher-gradual). Usher-strong density dependence leads to nonequilibrium dynamics for most values of E . Patterns

of elasticity change markedly when population dynamics undergo bifurcation (Grant and Benton, in press) and this in turn causes a change in the ESS life history. For example, crossing a bifurcation boundary from equilibrium dynamics to a two-cycle will lead to selection on the life history to dampen out the oscillatory dynamics and breed in low-density years (Grant and Benton, in press). Additionally, very different underlying dynamics can become very similar when noise is superimposed and thus cause similar stochastic ESS efforts, even when the deterministic ESS efforts were very different. See Grant and Benton (in press) for a fuller discussion of the relationship between elasticity, dynamics, and noise.

DISCUSSION

It is somewhat surprising that the impact of variation on the optimal life history is so apparent. *A priori*, one might expect density dependence to compensate for any environmentally driven fluctuations in the vital rates and thus cancel out their effect (Nicholson 1954). However, this appears not to be the case: environmentally driven variations in vital rates can cause marked changes in the optimal life history. The size and direction of the change in the optimum is extremely difficult to predict because it depends on a number of factors and how they interact: Similar levels of variability can cause the same life history to become more semelparous, more iteroparous, or change little depending on the combination of factors.

The early development of simple models investigating the impact of environmental variability (e.g., Schaffer 1974; see general review by Seger and Brockmann 1987) predicted that relatively greater variation in adult survival led to semelparous life histories, whereas greater variation in fecundity and juvenile survival led to iteroparous life histories. These results, as have been noted by Tuljapurkar (1989) and Orzack and Tuljapurkar (1989), apply only to a relative narrow range of life histories because of their lack of age structure. As found by Tuljapurkar and Orzack, variability can lead toward semelparity or iteroparity irrespective of the relative variability in the fecundities (which in discrete matrix models are products of the adult fertilities and juvenile survivorships) and adult survivorships.

A recent series of papers by Sasaki and Ellner (1995, 1997; Ellner and Sasaki 1996) has examined the issue of polymorphism in variable environments. In their models there is contest competition between juveniles and in each generation there is stabilizing selection on a trait, with an optimum value that fluctuates from year to year. For sufficiently large variance or sufficiently long-tailed distributions a “storage effect” occurs. This phenomenon leads to the differential adaptation of juveniles to different sorts of years. We use a monotonic trade-off curve. With such a trade-off it is difficult to generate multiple stable equilibria, for which more complex trade-off functions are needed (e.g. fig 8.8 in Stearns 1992). With more complex trade-offs, variation can maintain different optima through the storage effect even though in the deterministic situation there is a single ESS. In the models we used with a monotonic trade-off, multiple (local) ESSs did occur rarely. These only arose in deterministic situations

when the underlying dynamics were nonequilibrium and when different values of E were associated with different dynamical attractors and therefore different elasticities of ϑ . In such cases, the local ESSs were “played” against each other to find the global ESS (Rand et al. 1994; Schoombie and Getz 1998). In all cases a single global ESS was found; there were no cases of coexisting ESSs. Interestingly, in all cases the addition of noise abolished the local ESSs, leaving a single global ESS. In a recent paper, Van Dooren and Metz (1998) find something similar in a study of delay in germination: In a nonequilibrium constant environment coexistence of delay and nondelay strategies is possible, but in a noisy environment only a delaying strategy is stable.

Some generalizations are possible from the results presented here. First, the more costly reproduction is in terms of adult survival (the lower z), the greater the impact of a given level of variation. This is due to the nonlinearity of the trade-off, such that high survivorships are increasingly difficult to attain as z decreases. Imagine that average survivorship is 0.5, but varies from 0.3 to 0.7. By the time this survivorship is traded off—by multiplying it with $(1 - E^z)$ —when $E = 0.9$, the actual survivorship will vary from 0.09 to 0.17 when $z = 3$, but from 0.21 to 0.39 when $z = 9$. As the actual values of the survivorship decrease, there is a greater chance that whole cohorts will go extinct with the severe evolutionary consequences this will have. Most of our investigations have used $z = 6$ following Ricklefs (1977), who showed that for many species of birds z ranged from four to 10 with a mean of six. Since Ricklefs’s paper, there has been few other empirical estimates of z , so $z = 6$ is often used as a best guess (e.g., Erikstad et al. 1998). The imprecision of the estimate of z should be borne in mind: If z is commonly less than six, then the effect of environmental variability indicated here will be greater. Throughout we assumed that z was constant over time and that it was the vital rates that varied. However, it could also be that the cost of reproduction varied over time, as found, for example in Soay sheep (Stevenson and Bancroft 1995). Grant (unpubl.) found that, in the density-independent case, varying z stochastically had a marked impact on optimal effort, which can be more marked than variations in the vital rates themselves.

Second, “extreme” life histories (those with either very low or very high deterministic optimum efforts) tend to become less extreme under selection in a variable environment. Thus, when variation is high, most life histories end up with optimum efforts in the 0.7–0.8 range, irrespective of their deterministic optimum. With semelparous organisms, the risk of a whole cohort suffering reproductive failure (and thus having no descendants) in a bad year selects for some iteroparity, as bet-hedging suggests. Likewise, with organisms putting little effort into reproduction, variability selects for an increase in effort to minimize the risk of death before significant reproductive success is attained. Thus, semelparity is rarely favored by variability; equally, neither are extremely elongated reproductive lives.

Third, the vital rates upon which density dependence acts makes a considerable difference to the magnitude and direction that the effort changes in stochastic environments. That the optimal life history in a deterministic environment depends on the vital rates affected by density dependence has

previously been shown (Mylius and Diekmann 1995). However, additionally, our results also indicate that there is an interaction between the vital rates affected by density dependence and the impact of variation. Variation tends to decrease optimum effort when the survivorships are affected by density, but increase optimum effort when the fecundities are affected by density. This is presumably because having both density and environmental variability acting on the same vital rates means that they need to be “protected”; thus, more effort is put into those vital rates, trading off against the vital rates not affected by density. When density acts on fecundities, the net result is that the fecundities are more variable than survivorships due to the combination of density-independent and density-dependent forcing. Likewise, when density acts on survivorships, the result is that survivorships become more variable than fecundities. Simple application of bet-hedging models (e.g., Schaffer 1974) would suggest that in the former case iteroparity should be selected for and in the latter case semelparity. Our results indicate that iteroparity is almost always the ESS strategy under stochasticity. Only 3.5% of simulations ($n = 24$) resulted in semelparity. Of these, 20 were life histories where the deterministic optimum was also semelparity. The other four cases were for life history 14 (deterministic optimum 0.91) in relatively variable environments where the correlations between vital rates are all positive (so a bad year for fecundities is also a bad year for survival). Of the iteroparous optima, where fecundities vary more than survivorships (density dependence on F_S), the optimal effort tends to *increase* under variability (i.e., toward semelparity). The converse is true for situations where survivorships vary more than fecundities (density dependence on S ; see Figs. 7, 8). If anything, this change is the reverse of that predicted by the early models. For example, take an iteroparous life history (number 3) and density-dependent survival where the deterministic ESS effort is 0.75 (Table 1). If variability acts only on survivorship, naive application of the results of simple models suggest that semelparity would be favored in a variable environment. In fact, irrespective of the correlations between vital rates, the ESS effort in highly variable environments ($CV = 0.9$) only shows a modest increase to 0.77.

Fourth, the correlations between variations in the vital rates is important. If density-dependence affects the fecundities, then when the correlations are all strongly positive, the optimal effort tends to increase. Conversely, when there are negative correlations between fecundities and survivorships, the effort can increase, decrease, or remain similar to the deterministic effort. Presumably, if survivorships and fecundities covary positively, then a bad year for survival would also tend to mean reproductive output is low. Therefore, to avoid extinction of the genetic line, it might be better to invest more heavily in reproduction, so that at least if an individual does not survive it leaves some descendants. However, when fecundities and survivorships covary negatively, their effects can cancel out, thus causing little change from the optimum. In relatively semelparous organisms negative covariation can cause a decrease in effort. If an organism puts most effort into reproducing, then its fitness will be reduced in a bad year for fecundities—unless it can survive to reproduce again. However, if the reproductive effort is high anyway,

then even a good year for survival might represent a small chance of surviving to breed again. Thus, reproductive effort is decreased. In very iteroparous organisms, the correlation has less impact—all cause increases in effort. If density dependence acts on survivorship, then variation tends to cause optimum efforts to decrease. The smallest decreases occur with positive covariation, because the greatest semelparity is favored. When there is negative covariation, larger decreases in effort occur because greater iteroparity is favored.

We show here that stochasticity should be taken into account if an accurate adaptational analysis is desired. However, obtaining information on the environmental stochasticity is itself highly problematic. As in the density-independent case (Benton and Grant 1996), we show that infrequent catastrophic events can have a marked impact on fitness. Most biological studies do not last sufficiently long to estimate the environmental variance or the correlations between variations in the vital rates with any precision. The importance of long-term datasets in being able to indicate biologically realistic amounts of variation cannot be overstated. Factoring out the relative contributions of sampling error, demographic stochasticity, environmental stochasticity, and density dependence in the variation in the vital rates also makes precise analyses problematic. However, there is no doubt that variation occurs: For a range of animals and plants discussed in the literature, CVs for fecundity average 0.71 ± 0.38 (range 0.16–1.41) and for survival 0.39 ± 0.31 (range 0.10–1.41; Grant and Benton, unpubl.).

The change in ESS effort depends not just on the amount of variation, but also the correlations between variation in the different vital rates, the sampling distribution, the type of density dependence, where it acts in the life history, and the life history in question. The interactions between all these factors means that the response to increasing variation is not necessarily linear. Cooch and Ricklefs (1994) found that stochasticity has little impact on optimum effort, which is most likely a result of their using smaller CVs. We find that under moderate levels of variation, the shift in ESS effort is often within the range of $\pm 10\%$ of the deterministic ESS. This is a precision probably below that of an estimate of ESS effort based on field data, with its inherent sampling error. However, ESS effort *can* change markedly (up to 49%), especially in environments that are relatively variable or are subject to frequent catastrophic events. The latter is perhaps the most insidious; for example, a three-year field study could conclude that there was little environmental variation in vital rates, but miss the one-in-five yearly winter storms that decimates the population and has an untoward effect on ESS effort. For example, in an ongoing field study of wrens, *Troglodytes troglodytes*, M.R. Evans (pers. comm., 1997) found that an entire age class died out following the severe winter of 1995–1996.

The methods used here also allow us to compare ESS effort with the optimum predicted optimizing more traditional measures of fitness (such as population growth rate, r ; population size, reproductive success). These results are given in full elsewhere (Benton and Grant, unpubl.). In deterministic, equilibrium environments, the optima predicted using population size agree exactly with those predicted using ϑ , but those predicted using r maybe very different, as may those

predicted using R_0 if survival is density dependent. Conditions of low-to-moderate variability and equilibrium population dynamics optimizing population size (and when density affects fecundities alone, also R_0) produce a reasonably close approximation of the ESS effort (again, likely to be within the realms of uncertainty introduced by sampling error). However, in relatively variable environments, optimizing lifetime reproductive success or population size can produce poor to very poor estimates of the ESS effort. These results emphasize that there is no global definition of “fitness” as a quantity that natural selection maximizes. Individual fitness measures may work or they may not, and their use should be determined by how well they work (Stearns 1992). Fully accurate adaptational analyses should be based on invasibility criteria (Metz et al. 1992; Rand et al. 1994; Ferriere and Gatto 1995; Mylius and Diekmann 1995; Gurney and Middleton 1996; Schoombie and Getz 1998).

It is interesting to find an effect on the ESS fitness of the function relating density to the vital rates. This may well be linked with the strength of density dependence as the population fluctuates. If environmental variability causes populations to cross density thresholds or move from an area of steep slope (in the vital rate vs. density function) to an area of shallow slope, then this will add (intrinsic) variability to the population dynamics. As the different functions have different shapes, the effect of different functions (and/or different parameter choices within the same function, such that the underlying dynamics are characterized by different types of attractor) is unsurprising. Grant (1997) and Grant and Benton (in press) showed that with Ricker-models increasing the control parameter such that the attractor went from equilibrium to cycles to chaos caused marked changes in the elasticities of the vital rates. Therefore, the ESS life history depends on the underlying dynamics (Bulmer 1985; Van Dooren and Metz 1998; Schoombie and Getz 1998). It thus seems that variation in vital rates over time, whether caused by density dependence or environmental stochasticity, can have significant impacts on the evolution of life histories.

These results are based on density-dependent stochastic models and are broadly similar to recent results from density-independent stochastic models (e.g., Grant, unpubl.): Long-lived organisms may increase optimal effort, short-lived organisms may reduce optimal effort, but many organisms may have optimal efforts in a stochastic environment within about 10% of the optima in constant environments (see also Sibly et al. 1991; Cooch and Ricklefs 1994). We find here that the interquartile range for the percentage change in optimal effort (for CVs of > 0.5) is -12% to 9% , with only 17% of the data falling above $\pm 20\%$ change. This figure may increase markedly if the shape of the trade-off is changed, but generally if $z > 3-4$, it is unlikely that the picture will differ significantly.

LITERATURE CITED

- BEGON, M., M. MORTIMER, AND D. J. THOMPSON. 1996. Population ecology. 3d ed. Blackwell, Oxford.
 BENTON, T. G., AND A. GRANT. 1996. How to keep fit in the real world: elasticity analyses and selection pressures on life-histories in a variable environment. Am. Nat. 147:115–139.

- BULMER, M. G. 1985. Selection for iteroparity in a variable environment. *Am. Nat.* 126:63–71.
- CASWELL, H. 1989. Matrix population models. Sinauer, Sunderland, MA.
- CLUTTON-BROCK, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* 123:212–229.
- , ED. 1988. Reproductive success. Univ. of Chicago Press, Chicago.
- COOCH, E. G., AND R. E. RICKLEFS. 1994. Do variable environments significantly influence optimal reproductive effort in birds? *Oikos* 69:447–459.
- ELLNER, S., AND A. SASAKI. 1996. Patterns of genetic polymorphism maintained by fluctuating selection with overlapping generations. *Theor. Popul. Biol.* 50:31–65.
- ERIKSTAD, K. E., P. FAUCHALD, T. TVERAA, AND H. STEEN. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79:1781–1788.
- FERRIERE, R., AND M. GATTO. 1995. Lyapunov exponents and the mathematics of invasion in oscillatory or chaotic populations. *Theor. Pop. Biol.* 48:126–171.
- FOX, G. A. 1993. Life history evolution and demographic stochasticity. *Evol. Ecol.* 7:1–14.
- GRANT, A. 1997. Selection pressures on vital rates in density dependent populations. *Proc. R. Soc. Lond. B Biol. Sci.* 264:303–306.
- GRANT, A., AND T. G. BENTON. 2000. Elasticity analyses for density dependent populations in stochastic environments. *Ecology. In press.*
- GURNEY, W. S. C., AND D. A. J. MIDDLETON. 1996. Optimal resource allocation in a randomly varying environment. *Funct. Ecol.* 10:602–612.
- HACCOU, P., AND Y. IWASA. 1995. Optimal mixed strategies in stochastic environments. *Theor. Pop. Biol.* 47:212–243.
- LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities—a common mistake. *Auk* 104:116–121.
- METZ, J. A. J., R. M. NISBET, AND S. A. H. GERITZ. 1992. How should we define fitness for general ecological scenarios? *Trends Ecol. Evol.* 7:198–202.
- MURPHY, G. I. 1968. Pattern in life history and the environment. *Am. Nat.* 102:391–403.
- MYLIUS, S. D., AND O. DIEKMANN. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. *Oikos* 74:218–224.
- NICHOLSON, A. J. 1954. An outline of the dynamics of animal populations. *Aust. J. Zool.* 2:9–65.
- ORZACK, S. H. 1985. Population dynamics in variable environments. V. The genetics of homeostasis revisited. *Am. Nat.* 125: 550–572.
- ORZACK, S. H., AND S. TULJAPURKAR. 1989. Population dynamics in variable environments. VII. The demography and evolution of iteroparity. *Am. Nat.* 133:901–923.
- RAND, D. A., H. B. WILSON, AND J. M. McGLADE. 1994. Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* 343:261–283.
- RENSHAW, E. 1991. Modelling biological populations in space and time. Cambridge Univ. Press, Cambridge, U.K.
- RICKLEFS, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. *Am. Nat.* 111:453–478.
- SASAKI, A., AND S. ELLNER. 1995. The evolutionarily stable phenotype distribution in a random environment. *Evol.* 49:337–350.
- . 1997. Quantitative genetic variance maintained by fluctuating selection with overlapping generations: variance components and covariances. *Evolution* 51:682–696.
- SCHAFFER, W. M. 1974. Optimal reproductive effort in fluctuating environments. *Am. Nat.* 108:783–790.
- SCHOOMBIE, S. W., AND W. M. GETZ. 1998. Evolutionary Stable Strategies and trade-offs in generalised Beverton and Holt growth models. *Theor. Popul. Biol.* 53:216–235.
- SEGER, J., AND H. J. BROCKMANN. 1987. What is bet-hedging? *Oxf. Surv. Evol. Biol.* 4:182–211.
- SIBLY, R. M., AND P. CALOW. 1986. Why breeding earlier is always worthwhile. *J. Theor. Biol.* 123:311–319.
- SIBLY, R. M., L. LINTON, AND P. CALOW. 1991. Testing life-cycle theory by computer simulation. II Bet-hedging revisited. *Comp. Biol. Med.* 21:357–367.
- STEARNS, S. C. 1992. The evolution of life histories. Oxford Univ. Press, Oxford.
- STEVENSON, I. R., AND D. R. BANCROFT. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. *Proc. R. Soc. Lond. B Biol. Sci.* 262:267–275.
- TULJAPURKAR, S. D. 1989. An uncertain life: Demography in random environments. *Theor. Popul. Biol.* 35:227–294.
- . 1990a. Population dynamics in variable environments. Lecture Notes in Biomathematics no. 85. Springer, New York.
- . 1990b. Delayed reproduction and fitness in variable environments. *Proc. Nat. Acad. Sci.* 87:1139–1143.
- VAN DOOREN, T. J. M., AND J. A. J. METZ. 1998. Delayed maturation in temporally structured populations with non-equilibrium dynamics. *J. Evol. Biol.* 11:41–62.

Corresponding Editor: C. Boggs