Selection pressures on vital rates in density-dependent populations

ALASTAIR GRANT

School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

SUMMARY

For density-independent populations, the sensitivity of population growth rate to changes in individual vital rates indicates the strength of selection on different parts of the life history. Here I show how this approach may be extended to any density-dependent and/or stochastic population model, including those that show cyclic, quasi-periodic and chaotic dynamics. One calculates the influence of individual vital rates on the outcome of competition between two almost identical life histories. The outcome of this competition is determined by the invasion exponent ϑ introduced by Rand. This is the Lyapunov exponent of the linearized system describing the invasion of a population with one life history by a variant type with another. Demographic sensitivities are given by the partial derivatives of ϑ with respect to the individual vital rates of the invading type. The density-independent analysis is a special case of this general framework. Sensitivities can often be obtained analytically when the population has a stable equilibrium point, and can be calculated by numerical differentiation in other cases. One can also use the methodology to examine selection pressures on the parameters describing density dependence and, if there are trade-offs between vital rates, it can be used to determine optimal life histories. A two age-class example shows that the occurrence of nonlinear dynamics can markedly alter selection pressures on a life history from those which operate when the population has a stable equilibrium point.

1. INTRODUCTION

Sensitivity analysis is a powerful tool in demography and life history biology (Caswell 1989, 1996). For a matrix model, the influence of vital rates on density-independent population growth is indicated by the partial derivatives of the dominant eigenvalue λ with respect to m_{ij} , the individual elements of the projection matrix M :

$$\frac{\partial \lambda}{\partial m_{ij}}. \quad (1)$$

Sensitivities can be scaled to adjust for the different magnitudes of the vital rates, and are then referred to as elasticities (De Kroon *et al.* 1986). These can be calculated as:

$$\frac{m_{ij}}{\lambda} \frac{\partial \lambda}{\partial m_{ij}} = \frac{\partial \log \lambda}{\partial \log m_{ij}}. \quad (2)$$

This analysis can be applied to a projection matrix containing estimates of vital rates based on data from field or laboratory populations, giving insights into the selection pressures on, and demographic importance of, different parts of the life history. However, real populations of almost all species experience density-dependent population growth. It would therefore be of considerable interest to have an equivalent analysis for density-dependent populations, including populations with cyclic, quasi-periodic and chaotic dynamics.

2. ELASTICITIES FOR DENSITY-DEPENDENT POPULATIONS

For density-dependent and stochastic population models the dominant Lyapunov exponent of the population growth process is the analogue of $\log \lambda$ (Metz *et al.* 1992; Rand *et al.* 1994; Ferriere & Gatto 1995). Previous work (Benton *et al.* 1995; Benton & Grant 1996; Caswell 1996) has shown how sensitivities of this to individual vital rates can be calculated for stochastic density-independent models. We cannot, however, simply extend this approach to density-dependent models. Consider a population in which density dependence is of the type envisaged by the logistic equation, with a fixed carrying capacity. At equilibrium, the population size will be equal to the carrying capacity and the value of λ will be equal to 1. A small increase in the value of one of the vital rates will produce a change in the population age structure but density dependent effects mean that λ remains at 1, so all sensitivities would be equal to zero. We can only assess the fitness of a particular density-dependent life history relative to that of one or more competing life histories. The local optimality of a particular life history must be assessed using evolutionarily stable strategies (ESSs), and the term competitively stable strategy (CSS) has been used to denote a globally optimal life history (Hastings 1978*a, b*).

Recent work has shown how to assess the relative fitness of density-dependent life histories for any pattern

of dynamics (Rand *et al.* 1994; Ferriere & Gatto 1995). This can be used to obtain a generalization of sensitivity analysis that encompasses density-dependent models. Following Ferriere & Gatto (1995) we examine competition between a resident life history, R , and an alternative life history, a . If both types are present, then their dynamics are given by the coupled dynamic system:

$$x_R(t+1) = M[R, x_R(t), x_a(t)] x_R(t), \quad (3)$$

$$x_a(t+1) = M[a, x_a(t), x_R(t)] x_a(t), \quad (4)$$

where $M[R, x_R(t), x_a(t)]$ denotes the projection matrix for type R as a function of $x_R(t)$ and $x_a(t)$, the population vectors for type R and type a respectively. The ESS is determined by examining the linearized dynamics of this system at the point $x_a(t) = 0$. a can invade if the largest Lyapunov exponent of the matrix sequence $\{M[a, 0, x_R(t)]\}$ is positive. Ferriere & Gatto (1995) use the symbol $S_R(a)$ for this quantity and Rand *et al.* (1994) refer to it as the invasion exponent, ϑ . I use the latter in the remainder of this paper.

Consider the case in which R and a have identical life histories and individuals of one type contribute to the density dependence of the other population in exactly the same way as do individuals of the population itself. Here, $\vartheta = 0$, and the two types coexist indefinitely. For biologically plausible life histories, increasing any one of the values of the vital rates of the alternative life history will lead to ϑ being greater than 0, so a can invade. The rate at which invasion occurs indicates the sensitivity of the population growth process to that element of the life history and thus quantifies the selection pressure on it. In more formal terms, the analogue of the elasticity is given by $\partial\vartheta/\partial \log m_{ij}$ and the analogue of the sensitivity by $\partial \exp[\vartheta]/\partial m_{ij}$. If the resident population has a stable equilibrium point, x_R is constant. ϑ is then the logarithm of the dominant eigenvalue of $M[a, 0, x_R]$, the projection matrix for the invading type when its population is zero and that of the resident type is at its equilibrium. Analytical expressions for the partial derivatives can then often be found. For other patterns of population dynamics, including chaos, they can be evaluated by numerical differentiation. Density-independent sensitivities are a special case of this general framework. In the absence of density dependence, the projection matrix, M , is independent of the abundance of either type, and ϑ is equal to $\log \lambda$ for this constant matrix. Sensitivities and elasticities are then given by equations (1) and (2).

3. AN EXAMPLE

We illustrate the calculation of elasticities using a two age-class model of a fishery (Levin 1981; Caswell 1989, example 9.5). The projection matrix is:

$$M = \begin{pmatrix} \mu \exp(-\beta N) & 2\mu \exp(-\beta N) \\ P & 0 \end{pmatrix}, \quad (5)$$

where N is the sum of numbers in the two age classes and β indicates the strength of density dependence. If $\beta = 0.1$ and $P = 0.9$ then for small values of the control

parameter μ the model has a stable equilibrium point. It then displays a Hopf bifurcation to quasi-periodic dynamics at $\mu \approx 11.458$ and as μ is increased still further, the dynamics become chaotic. The equilibrium point is given by:

$$N = \frac{\log[\mu(1+2P)]}{\beta}. \quad (6)$$

If the equilibrium is stable, we can substitute this expression into (5) and determine partial derivatives of λ with respect to individual vital rates. So, for example, we obtain:

$$\frac{\partial \lambda}{\partial P} = \frac{2}{1+4P}. \quad (7)$$

As $\lambda = 1$ the elasticity is given by

$$P \frac{\partial \lambda}{\partial P} = \frac{2P}{1+4P}. \quad (8)$$

In the same way, the elasticity for the density-dependence parameter β is

$$\frac{\partial \log \lambda}{\partial \beta} = - \frac{(1+2P) \log(\mu[1+2P])}{1+4P}. \quad (9)$$

4. NUMERICAL DIFFERENTIATION WHEN THE EQUILIBRIUM IS NOT STABLE

When the resident population is subject to stochastic variation of vital rates, or has cyclic, quasi-periodic or chaotic dynamics we need to use numerical differentiation, approximating the elasticity by $\Delta\vartheta/\Delta m_{ij}$. We begin with an arbitrary population vector of the resident type and a projection matrix M in which the density-dependent elements are a function only of the population vector of R . We then iterate the recurrence relationship:

$$x_R(t+1) = M x_R(t), \quad (10)$$

until the population stabilizes on the attractor (which may or may not be a single equilibrium point, depending on the vital rates and the nature of the density dependence). Then we introduce an alternative type, setting the population vector for this to an arbitrary starting point. $M^\#$, the projection matrix for the alternative type, is identical to M , with the exception that one of the elements of M is increased by multiplying it by $(1+\delta)$, where δ is a small increment. For the example population, to calculate the elasticity for the fecundity of the first age class we use the projection matrix:

$$M^\# = \begin{pmatrix} (1+\delta)\mu \exp(-\beta N) & 2\mu \exp(-\beta N) \\ P & 0 \end{pmatrix}. \quad (11)$$

We want to evaluate the dynamics at the point where the invading population is equal to zero. We therefore do not allow a to contribute to density dependence, and consider only the influence of the population vector of R on the density-dependent elements of $M^\#$. So, for the example population, the

Table 1. Elasticity values for the projection matrix in equation (5) for three values of the parameter μ . Elasticities for $\mu = 4$ were obtained using analytical results, the others using numerical differentiation

parameter value	$\mu = 4$	$\mu = 12$	$\mu = 25$
dynamics	stable equilibrium	quasi-periodic	chaotic
elasticity values	0.217 0.391 0.391 0	0.223 0.389 0.389 0	0.351 0.321 0.321 0
elasticity for β	-1.47	-2.12	-2.56

value of N in $M^\#$ includes only the numbers of type R . We then determine ϑ the invasion exponent for the coupled system:

$$x_R(t+1) = Mx_R(t), \quad (12)$$

$$x_a(t+1) = M^\#x_a(t), \quad (13)$$

using the expression:

$$\vartheta = \lim_{t \rightarrow \infty} \frac{1}{t} \{ \log(N_a(t)) - \log(N_a(t)) \}. \quad (14)$$

The invasion is exponential, but nonlinear dynamics of the resident type produce fluctuations around this trend. ϑ can therefore be most accurately estimated by the slope of the least squares regression of $\log N_a(t)$ on t (Rand *et al.* 1994). The numerical differentiation involves calculating:

$$\frac{\vartheta(M) - \vartheta(M^\#)}{\log(m_{ij}) - \log(m_{ij}(1+\delta))}, \quad (15)$$

where $\vartheta(M) = 0$, so this formula for the elasticity reduces to $\vartheta(M^\#)/\log(1+\delta)$. This process is then repeated for the other non-zero elements of M . For some patterns of chaotic dynamics, small values of δ can produce large numerical errors in the elasticities for manageable numbers of iterations. I have, in consequence, used a value of 0.01 for δ in the calculations reported here. Checking that the sum of elasticities for vital rates is near to 1 provides a useful precaution against such problems.

Elasticities for three values of μ for the example model are shown in table 1, and elasticities for the survival rate P are plotted against μ in figure 1*a*. As noted above, elasticities are independent of μ when the equilibrium is stable. At equilibrium, population growth is zero, so offspring produced at any age are of equal value. There is a high probability of survival from age 1 to age 2, so the elasticities for the fecundities reflect the fact that the fecundity of the second age class is greater than that of the first age class. Proportional increases in the single survival probability and in fecundity at age 2 have the same effects, so their elasticities are equal. Once μ is increased beyond the bifurcation, the elasticity for the fecundity at age 1 begins to increase and those for the other two vital rates decrease. When $\mu = 12$, the difference is only about 2%, but the elasticities alter markedly at $\mu \approx 12.92$ and then continue to change more gradually. For $\mu > 20$ there is considerable scatter about this trend (see figure 1*a*). For large values of μ , the elasticity for the fecundity at age 1 is greater than that for the other two vital rates. Clearly the occurrence of nonlinear

Figure 1. (a) Influence of the control parameter μ on elasticities for the survival rate P for the example population model described in the text. (b) Influence of μ on the elasticity for the density dependence parameter β in the same model.

dynamics can have a marked influence on the selection pressures on life histories. Elasticities for β are plotted against μ in figure 1*b*. Selection pressure on β is much stronger than that on individual vital rates, and this becomes more marked as the value of μ is increased. Even when the dynamics are chaotic, elasticities for β calculated numerically are close to the values obtained using equation (9).

5. CONCLUSION

The results presented here allow selection pressures on density-dependent life histories to be assessed, extending this powerful tool to all populations. The example demonstrates that the nature of population dynamics can be an important influence on selection pressures. The methods can also be used to determine locally optimal life histories for any pattern of density dependence. If the projection matrix is parametrized in terms of reproductive efforts, and trade-offs between life history traits are introduced, then an ESS life

history is one for which the sensitivities of ϑ to changes in reproductive effort are zero. If there is more than one ESS, then the CSS can be determined by examining the invasion of each ESS by all others. The application of these methods to a wider range of life histories will be presented elsewhere.

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