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The Evolution of Oscillatory Behavior in Age-Structured Species

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abstract: A major challenge in ecology is to explain why so many species show oscillatory population dynamics and why the oscillations commonly occur with particular periods. The background environment, through noise or seasonality, is one possible driver of these oscillations, as are the components of the trophic web with which the species interacts. However, the oscillation may also be intrinsic, generated by density-dependent effects on the life history. Models of structured single-species systems indicate that a much broader range of oscillatory behavior than that seen in nature is theoretically possible. We test the hypothesis that it is selection that acts to constrain the range of periods. We analyze a nonlinear single-species matrix model with density dependence affecting reproduction and with trade-offs between reproduction and survival. We show that the evolutionarily stable state is oscillatory and has a period roughly twice the time to maturation, in line with observed patterns of periodicity. The robustness of this result to variations in trade-off function and density dependence is tested.

Keywords: age-structured populations, periodicity, delayed density dependence, adaptive dynamics, evolutionarily stable strategy.

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One of the key findings of classical ecological theory is that even simple population models can show a rich range of dynamical behavior, from asymptotically stable equilibria right through to chaos (May 1974). Whether this theoretical richness in behavior reflects what we see in nature is, however, an open question. For example, despite an understandable and considerable interest in the phenomenon of chaos, very few population dynamical time series are convincingly chaotic (as opposed to noisily periodic; Grover et al. 2000; Turchin and Ellner 2000; Bjørnstad and Grenfell 2001). Rather, most field populations exhibit apparently stable or cyclic population dynamics (e.g., Clutton-Brock et al. 1997; Sæther 1997; Wickens and York 1997; Kendall et al. 1998; Siriwardena et al. 1998; Bjørnstad et al. 1999; Fewster et al. 2000; Freckleton and Watkinson 2002). In fact, approximately 30% of ecological systems for which reliable and sufficiently long time series are available are periodic or near periodic (Kendall et al. 1998).

There has been considerable divergence of opinion about the cause (or causes) of this periodicity. Interaction with the environment provides one possible explanation, either through periodicity in the environment (e.g., seasonality) or by noise in the environment exciting and amplifying natural modes of oscillation (Nisbet and Gurney 1976; Greenman and Benton 2003, 2005). However, more attention has been given to interaction between trophic layers as a possible source of periodicity. Familiar examples include the 10-year cycle in the time series for the snowshoe hare in northern Canada, with lynx as the predator (Elton and Nicholson 1942; Stenseth et al. 1997; King and Schaffer 2001), the 3–5-year cycle of small rodents in northern Fennoscandia (Hansen et al. 1999; Stenseth 1999; Schaffer et al. 2001), subject to specialist predation, and the larch budmoth 9-year cycle identified in the forests of the Swiss Alps, with parasitoid predation and resource quality the key factors (Turchin et al. 2003). Predation through parasites and parasitoids defines a special class of trophic interaction and hence a possible explanation of periodicity. A well-known example where this mechanism has been demonstrated (Hudson et al. 1998) is the erad-

ication of cycles in red grouse (on one site in the north of England) by vaccination against the parasite *Trichostrongylus tenuis*.

Even though in practice a population is necessarily part of a trophic web, the primary source of its periodicity may still be intrinsic rather than through its interactions with other components in the web. This is the argument of Inchausti and Ginzburg (1998) in their discussion of the 3-year vole cycle of northern Fennoscandia. They focus on the "quality" of the offspring (i.e., the maternal effect) as the driving force behind the observed oscillations. Further, in a recent article (Murdoch et al. 2002), it has been argued that a generalist consumer in a food web can be modeled by a single-species model (when abundant resources are available), whereas specialist consumers require multilevel analysis. The generalist can switch to other resources and maintain consumption if there is a shortfall in particular resources, thus averaging out the variations in the environment. Their review of the literature showed that when oscillations occur, the periods for the generalist consumers are typically less than four times the time to maturation (MT), while specialist consumers have a period lying above this range.

To explain the patterns of periodicity that have been observed in actual populations is a major challenge. Models show that for structured single species, a large range of periodic modes of oscillation can be accessed (Greenman and Benton 2004), whereas in the field the periods appear to be narrowly limited. One explanation is that evolution constrains the population dynamics that can occur (Metz et al. 1996; Geritz et al. 1998). We examine this hypothesis by analyzing a family of age-structured single-species matrix models with reproduction diminished by adult-driven density dependence and with embedded life-history trade-offs between reproduction and survival. We show that under certain conditions, species described by such models evolve to a fluctuating evolutionarily stable state (ESS; Maynard Smith 1982) at which the population oscillates with a period that conforms to the patterns seen in nature (Murdoch et al. 2002).

The dynamics of the evolutionarily stable state (ESS) have also been studied by others, using age-structured matrix models (Leslie 1945; Caswell 2001). Ferriere and Gatto (1993), for example, showed that a chaotic ESS is possible, while Ebenman et al. (1996), using different density-dependent and trade-off structures, showed that selection will often lead to more stable populations.

The Fundamentals

The basis of our analysis is the discrete time age-structured population model:

$$\begin{aligned} x_{t+1} &= \phi z_t \exp(-N_{rt}), \\ y_{t+1} &= \gamma x_t, \\ z_{t+1} &= \gamma y_t + \sigma z_t, \\ N_{rt} &= c_1 x_t + c_2 y_t + z_t, \end{aligned} \tag{1}$$

where populations x_t, y_t, and z_t denote the number of "juveniles," "subadults," and "adults," respectively, at time t, ϕ represents the per capita reproduction rate of adults, and γ and σ represent the per capita survival rates of their respective populations. The parameters c_1 and c_2 measure the contribution of preadult stages to density dependence. All but the reproduction parameter ϕ lie in the interval $0 \le c_1, c_2, \gamma, \sigma < 1$.

There are various ways in which density dependence can be included in a Leslie-style structured population model (Leslie 1945). Neubert and Caswell (2000), for example, consider four variations of a 2 × 2 structured model with density dependence affecting the component populations through fecundity, growth, and subadult and adult survival (Caswell 2001). In practice, it has proved difficult to clearly identify through which vital rates density dependence works. However, there has been some evidence that adult survival is not the primary mechanism and that, for a range of species, fecundity and juvenile survival in the first year are the rates most sensitive to density effects (Gaillard et al. 1998; Tripet and Richner 1999). In our model, we will follow this empirical evidence and apply density dependence only to reproduction (including first-year survival) in the first equation of model (1). With parameters c_1 and c_2, the contribution of the preadult stages to this nonlinearity can be examined.

The key question is, which parts of the parameter space of the model are biologically relevant? Not all points of this space are likely to be feasible, because of implicit relationships that may exist between parameters arising, for example, from mass-energy balances (DeLeo and Dobson 1996; West et al. 1997; Koojiman 2000), and the choice will be furthered restricted by evolutionary selection. In order to model evolution, we take the standard approach of assuming that populations evolve through time as a result of invasion by fitter rare mutants. At each invasion the mutational change is taken to be small. This is the adaptive-dynamics approach (Metz et al. 1996; Geritz et al. 1998), and it can be studied by invasion analysis. Typically, the trait is described by one of the model parameters, but it is reasonable to assume that other parameters in the model are likely to be affected by mutational changes in this trait because of the existence of trade-offs between parameters. Higher levels of per capita reproduction (ϕ), for example, might imply a lower level of adult survival (σ). Such trade-offs are well studied both empirically and

theoretically (Stearns 1992; Roff 2002) and underpin evolutionary theory.

For situations where the resident species is in stable equilibrium when alone, the invasion criteria can often be established algebraically. However, in those situations where the resident is in an oscillatory state (Ferriere and Gatto 1993), one has to proceed either by exhaustive simulation to determine which species survives asymptotically or, more efficiently, by applying the leading Lyapunov exponent criterion for invasion. This exponent provides us with a generalization for the concept of eigenvalue when a system is unstable (Ferriere and Gatto 1993). The exponent is calculated from the Jacobian of the equations for the mutant species, linearized about a zero-mutant population because the number of invading mutants is assumed to be small. The effect of fluctuations in the resident component populations is to render certain of the mutant parameters, and hence the mutant Jacobian, time dependent. Precisely, the leading Lyapunov exponent (ξ) is calculated from the formula

$$\xi = \lim_{t\to\infty}\left[\left(\ln \| M_{t-1}M_{t-2}M_1M_0k \|\right)/t\right], \tag{2}$$

where M_t is the mutant Jacobian at time t, k is a randomly chosen vector, and the vector length ($\|\ldots\|$) in formula (2) can be taken to be Euclidean. Leading exponent ξ can be interpreted as a measure of mutant fitness (relative to that of the resident). If it is positive, the mutant can invade the environment set by the resident; if it is negative, invasion is not possible.

When parameters fluctuate, one might be tempted to think that standard invasion criteria would apply after a simple averaging of parameters. However, there are many ways of "averaging" and different functions that can be averaged. Formula (2) tells us exactly how to carry out the averaging. It reduces to the standard formula when the resident is stable or oscillates with integer period.

A sequence of successful invasions (with exclusion of the resident species) can lead to an evolutionarily stable state (ESS; Maynard Smith 1982) where the resident is uninvadable by other strains. This is what happens for model (1). To locate the position of its ESS in parameter space, we assume that the competition between resident and mutant populations acts only through the density-dependent terms:

$$\begin{aligned} u_{t+1} &= \phi' w_t \exp\left[-(N_{mt} + N_{rt})\right], \\ v_{t+1} &= \gamma' u_t, \\ w_{t+1} &= \gamma' v_t + \sigma' w_t, \\ N_{rt} &= c_1 x_t + c_2 y_t + z_t, \\ N_{mt} &= c_1' u_t + c_2' v_t + w_t. \end{aligned} \tag{3}$$

Here u_t, v_t, and w_t denote the mutant component populations and ϕ', c', γ', and σ' the perturbed parameters for the mutant. We also assume that there are trade-offs operating between reproduction and adult survival. For definiteness, we take them to be of the form

$$\sigma = \sigma_0[1 - (\phi/\phi_0)^2], \tag{4a}$$

$$\sigma' = \sigma_0[1 - (\phi'/\phi_0)^2], \tag{4b}$$

for the resident and mutant, respectively, with σ_0 and ϕ_0 constant in both cases. With this choice of function, higher reproduction becomes increasingly costly in terms of adult survival. The other parameters in the model are kept fixed, with resident and mutant values taken as equal. In particular, we initially suppose that density dependence is a function only of the adult populations (i.e., $c_1 = c_2 = c_1' = c_2' = 0$). When linearized about the zero-mutant population state, equations (3) take the form

$$\begin{aligned} u_{t+1} &= \phi' w_t \exp(-N_{rt}), \\ v_{t+1} &= \gamma' u_t, \\ w_{t+1} &= \gamma' v_t + \sigma' w_t. \end{aligned} \tag{5}$$

The mutant Jacobian, M_t, can be read off from equation (5) once the dynamics (x_t, y_t, z_t) of the resident alone have been determined. The leading Lyapunov exponent is then calculated from formula (2).

Typical results are shown in the pairwise invadability plot (PIP; Geritz et al. 1998) of figure 1. This plot shows the positioning of the zero-fitness curve (i.e., where the exponent ξ is 0) in (ϕ, ϕ') space. There are two branches of this curve: the radial line (because then the mutant is identical to the resident) and a nonlinear curve that is roughly hyperbolic in shape. The region between these branches is the region where the mutant can invade. The point of intersection of these branches identifies the position of the ESS. That it is an ESS, implying invulnerability to further attack, follows from the positioning of the invasion regions with respect to the (singular) intersection point. A full classification of PIP intersection points is given in Metz et al. (1996) and Geritz et al. (1998).

Tracking Evolution in Parameter Space

At each stage in the adaptive dynamical process, the current resident species can be identified by its location in parameter space, and hence the process itself can be represented by a sequence of points, that is, a trajectory in this space. Of interest is the shape of this trajectory and its positioning in relation to the stability region of model (1). Above all we are interested in the position of the end

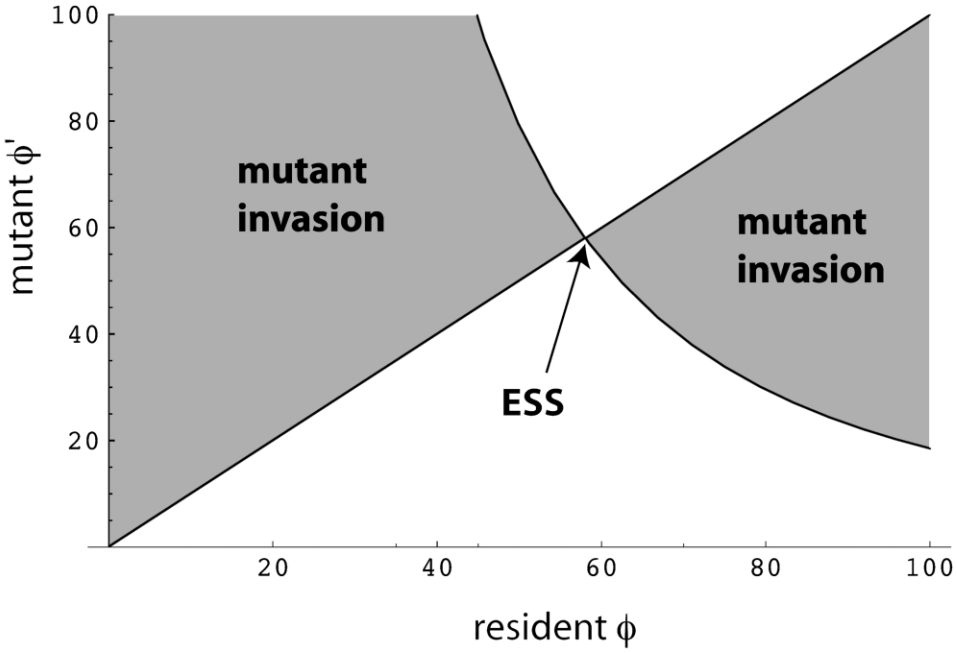

Figure 1: Pairwise invadability plot for model (1), with a single trade-off relating adult survival to per capita reproduction (see eqq. [4]). Parameters: $\phi_0 = 100.0$, $\sigma_0 = 0.5$, $\gamma = 0.5$, and $c_1 = c_2 = 0$ (i.e., density dependence is a function only of adult population).

(limit) point of this trajectory where the species has finally reached evolutionary equilibrium, whether it lies inside or outside the stability region. We will refer to this equilibrium point as the ESS point.

To locate the stability region, it is convenient to take the coordinates of parameter space to be not the parameters of the model but the coefficients of the equation for its eigenvalues when linearized about the equilibrium point (Greenman and Benton 2003). For the 3×3 model (1), the eigenvalue equation is

$$\lambda^3 - u\lambda^2 - v = 0, \tag{6}$$

where u is the trace and v the determinant of the Jacobian of model (1), linearized about its point equilibrium. Coefficients u and v are functions of the model parameters ϕ, γ, and σ. In fact, with $c_1 = c_2 = 0$ and z_0 the adult equilibrium level,

$$\begin{aligned} u &= \sigma, \\ v &= \gamma^2\phi(1 - z_0)\exp(-z_0), \\ z_0 &= \ln[\phi\gamma^2/(1 - \sigma)]. \end{aligned}$$

The stability region is bounded by three curves corresponding to the three ways in which the model can become unstable. The curves are defined by the condition that the modulus of the dominant eigenvalue(s) (i.e., the eigenvalue[s] with largest modulus) is equal to 1. (The modulus of a complex number $a + ib$ is given by $[a^2 + b^2]^{1/2}$.) The "period-doubling" boundary consists of those points where the dominant eigenvalue equals -1, while the "extinction" boundary corresponds to dominant eigenvalue $+1$. The third boundary, the "quasi-periodic" boundary, is defined by those points where the model has a pair of complex conjugate eigenvalues with modulus 1. In figure 2*A*, we show the stability region in (u, v) space bounded by these three curves. The period-doubling and extinction boundaries are the straight lines, $v + u = \pm 1$, and the quasi-periodic boundary is a hyperbola with equation $1 + uv - v^2 = 0$. There are four corners to this stability region (*P*, *Q*, *R*, and *S*) where the boundary sections intersect. At two of these corners, there is a jump in the period of the dominant eigenvalue as the corner is traversed on the boundary. (Note that the period of an eigenvalue $a + ib$ is given by $2\pi/\theta$, where $\theta = \tan^{-1}[b/a]$, so eigenvalue -1 has period 2 and eigenvalue $+1$ has infinite period.) At corner *P*, the jump is from period 2 to period 6, and at *R* it is from period 3 to period infinity. There is also a gap in the periods of the dominant eigenvalues that are achievable on the boundary of the stability region. For model (1), there is no boundary point where this period lies between 3 and 6 (fig. 2*A*). However, there are points on extensions of the quasi-periodic boundary

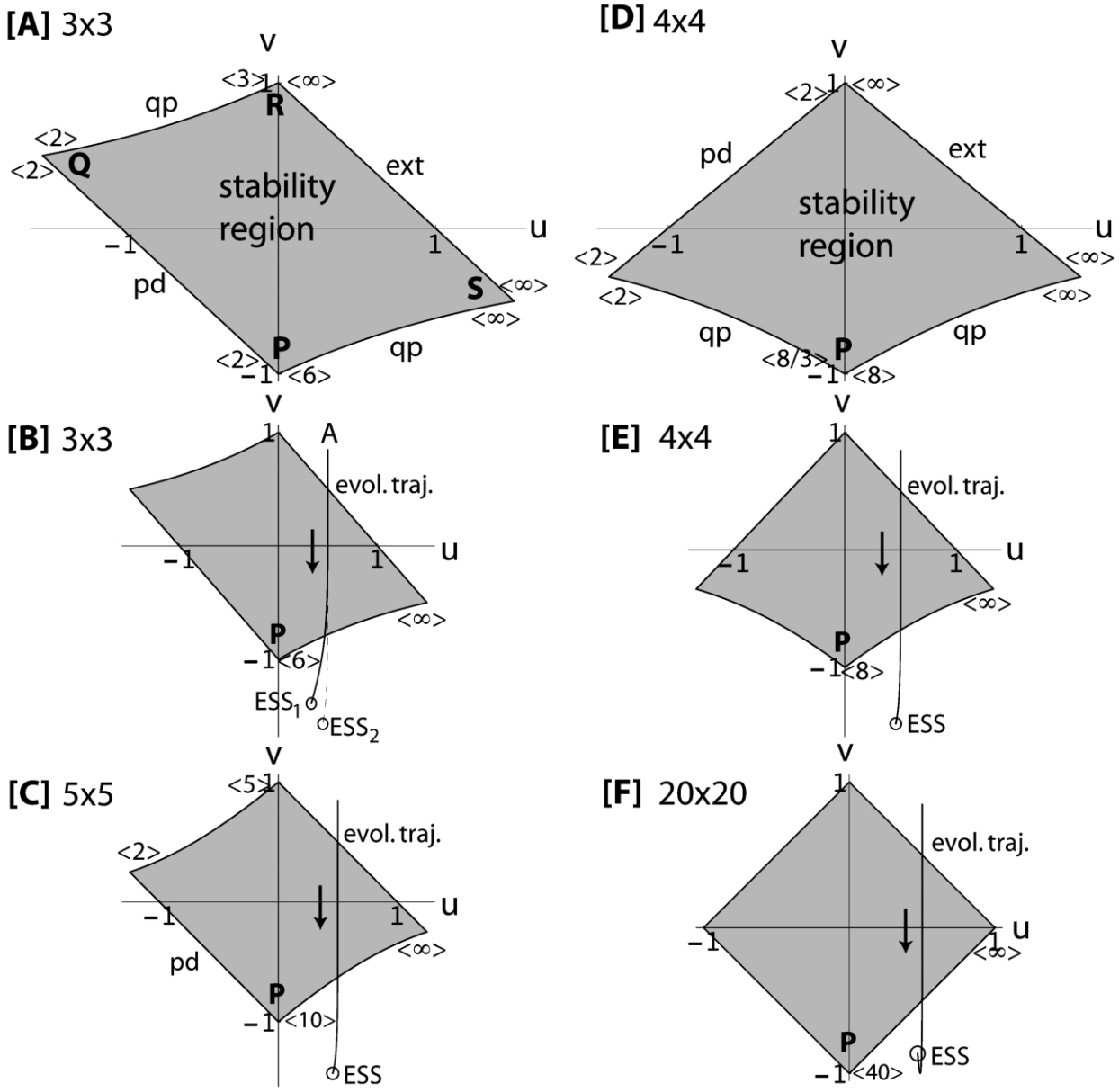

Figure 2: Stability regions, evolutionary trajectories (*evol. traj.*), and evolutionarily stable states (*ESS*) in (u, v) eigenvalue coefficient space for (*B*) 3 × 3, (*C*) 5 × 5, (*E*) 4 × 4, and (*F*) 20 × 20 age-structured models. All trajectories are for double trade-offs except in *B*, where ESS_1 is for a single and ESS_2 for a double trade-off. *A*, Stability region in more detail for the 3 × 3 case (typical of odd-dimensional models). *D*, Details for the 4 × 4 case (typical of even-dimensional models). Boundary section end point periods shown in carets. Parameters: $\phi_0 = 100.0$ and $\sigma_0 = 0.5$; $\gamma_0 = 1.0$ for double and $\gamma = 0.5$ for single trade-off. In all cases, density dependence is a function only of adult population (i.e., $c_1 = c_2 = 0$). Boundaries: qp = quasi-periodic; pd = period doubling; ext = extinction.

beyond the stability region where these periods do occur, but they are then periods of subdominant eigenvalues.

As the names suggest, crossing the extinction boundary leads, in general, to extinction of one or more of the age classes and thus to extinction of the population as a whole, while crossing the period-doubling boundary leads to instability, initially through period 2 cycles and thence through a succession of period doublings to chaos as the distance from the boundary increases. Crossing the quasi-periodic boundary initially leads to nonchaotic oscillations, either periodic (with integer period) or quasi-periodic. (A precise definition of quasi periodicity can be

found in Katok and Hasselblatt 1998.) Quasi-periodic oscillations can be associated with a noninteger period by locating the position of the sharp power spike dominating the frequency spectrum (Jenkins and Watts 1969; Greenman and Benton 2005). The areas adjacent to the quasi-periodic boundary where the system executes strictly periodic oscillations are called Arnol'd tongues and have "exotic" shapes. For details, see Arnold (1983) and Greenman and Benton (2004).

Shown in figure 2*B* is the trajectory followed by the species as trait ϕ is progressively increased (with trade-offs in eq. [4] operating and density dependence a function only of adult population). The trajectory starts (when $\phi = 1.0$) at point *A* with populations extinct, reproduction being too low to sustain the populations. With increase in ϕ the trajectory crosses the stability region to exit through the quasi-periodic boundary near corner *P*. It reaches its ESS point (denoted by ESS_1 for a single trade-off) when $\phi = 58.0$ (read off from fig. 1). At this ESS point, the asymptotic behavior of the system is quasi-periodic, with period close to the eigenvalue period at corner *P*, namely, period 6. This is twice the time to maturation for the 3 × 3 model (1).

How Robust Are These Properties?

So far we have assumed a single "reproductive effort" trade-off relationship, between fecundity ϕ and adult survival σ. However, there are also likely to be trade-offs between the fecundity and quality of offspring (Fox and Czesak 2000), leading to maternal effects on offspring survival and growth. Such maternal effects are known to be prevalent for a wide range of organisms (Mousseau and Fox 1998). Therefore, changing fecundity can lead to correlated changes in the subadult traits (through the number-quality trade-off) as well as changes in the adult traits (through the reproductive effort trade-off). Such patterns of interconnected trade-off relationships are expected to be common (Roff 2002). The number-quality trade-off can be modeled with a function in the form of equation (4a), with σ replaced by γ:

$$\gamma = \gamma_0[1 - (\phi/\phi_0)^2], \tag{7}$$

with γ_0 and ϕ_0 constant. Modeling multiple trade-offs needs to be undertaken with care. In some situations complex and potentially biologically unrealistic relationships between two traits can be created if both are traded off against a third trait. Under our assumptions (eqq. [4] and [7]), this does not happen. Adult and subadult survival, σ and γ, respectively, are always positively correlated.

With both trade-offs acting, the species follows a trajectory that only deviates from that for a single trade-off as the ESS point (denoted by ESS_2 for a double trade-off) is finally approached (fig. 2*B*). The two ESS points, for single and double trade-offs, are seen to lie close together.

Sensitivity of these results to variation in the (otherwise fixed) parameters γ (single trade-off) and σ_0 (double trade-off) is given in table 1. We note in particular that the position of the ESS point in (u, v) space is reasonably robust to the number of trade-offs but the value of the trait ϕ at the ESS point is not. With a double trade-off, the model predicts a much lower level of fecundity in the fully evolved species. Numerical testing also shows that the ESS position is insensitive to variation in the trade-off benchmark parameter ϕ_0 (in eqq. [4] and [7]), with ϕ approximately scaling with ϕ_0.

Higher Dimensional Models

The result that the period is roughly twice the time to maturation, established in the 3 × 3 case, generalizes to higher dimensions. Consider, for example, the following five-stage model based on model (1) with two extra subadult stages, p_t and q_t, added,

Table 1: Sensitivity analysis of evolutionarily stable state (ESS) position and period with respect to density dependence (dd) and trade-off structure for model (1)

Single trade-off ($\phi \to \sigma$)			Double trade-off ($\phi \to \sigma$, γ)		
γ	ϕ at ESS[a]	ESS period	σ_0	ϕ at ESS[b]	ESS period
Density dependence with adults only ($c_1 = c_2 = 0$)					
.7	49	6.9	.7	28	7.9
.5	58	6.6	.5	32	6.8
.3	91	6.3	.3	38	6.3
Density dependence with all three stages[c]					
.7	49	6.2	.7	32	6.8
.5	59	eqm	.5	35	6.0
.3	59	eqm	.3	41	5.6
Density dependence with adults and subadults only[d]					
.7	43	5.8	.7	31	6.2
.5	51	4.9	.5	32	5.8
.3	57	4.1	.3	33	5.1

Note: ESS location and period for model (1).

[a] $\sigma_0 = 0.5$ for rows 1–3 and 0.75 for all other rows.

[b] $\gamma_0 = 1.0$ for all rows.

[c] For dd with all three stages, $c_1 = c_2 = 0.1$. Equilibrium (eqm) is possible with low γ or low σ_0. For higher c_1, c_2, ESS is no longer possible for any parameter values.

[d] For dd with adults and subadults only, $c_1 = 0$ and $c_2 = 0.5$. ESS is always quasi-periodic unless γ or σ_0 is exceptionally low.

$$\begin{aligned} x_{t+1} &= \phi z_t \exp(-z_t), \\ y_{t+1} &= \gamma x_t, \\ p_{t+1} &= \gamma y_t, \\ q_{t+1} &= \gamma p_t, \\ z_{t+1} &= \gamma q_t + \sigma z_t, \end{aligned} \tag{8}$$

and density dependence a function only of adult population. We suppose that there are two trade-offs, between reproduction and adult and subadult survival. The eigenvalue equation for model (8) is given by

$$\lambda^5 - u\lambda^4 - v = 0,$$

where, again, u is the trace and v the determinant of the model Jacobian. In (u, v) space the stability region is as shown in figure 2*C* with the "evolutionary" trajectory superimposed. Again, there is a quasi-periodic ESS point outside the stability region near the corner (P) of the quasi-periodic stability boundary where the eigenvalue period is 10, twice the time to maturation. At this corner there is a jump in dominant eigenvalue period from 2 to 10. (There is also a gap from 5 to 10 in the period achievable on the stability boundary.)

In general, for a model with an odd number $(2n + 1)$ of stages, the eigenvalue equation is $\lambda^{2n+1} - u\lambda^{2n} - v = 0$, and its stability region in (u, v) space has a corner, P, with a period jump from 2 to $(4n + 2)$ and a boundary period gap from $(2n + 1)$ to $(4n + 2)$, generalizing the properties shown in figure 2*A*–2*C*. Lyapunov exponent calculations confirm that, certainly up to $n = 9$, there exists a quasi-periodic ESS point that lies close to this corner, P, and with period close to 2MT, where MT $= 2n + 1 =$ time to maturation.

If there are an even number $(2n)$ of stages, then the stability region has a similar structure, but the corners are formed by the intersection of different boundary sections (see fig. 2*D*, 2*E* for $n = 2$ and fig. 2*F* for $n = 10$). However, the ESS point still lies close to a corner of the stability region boundary where the period is twice the time to maturation, and this property certainly holds up to $n = 10$.

We have carried out sensitivity analysis at these higher dimensions with respect to variations in parameter values and the number of trade-offs, and as in the 3 × 3 case, the twice-maturation time rule has proved reasonably robust to these changes.

Density-Dependent Structure

So far we have considered per capita reproduction reduced only by competition between adults ($c_1 = c_2 = 0$). Whether our results hold in the more general case, where preadult stages also contribute to the density dependence, is a question we have studied in some detail, but restricting attention to the 3 × 3 case. If preadult stages contribute only to a small degree ($c_1 = c_2 = 0.1$), then table 1 shows that, with a single trade-off, the ESS point can lie within the stability region but, for both trade-offs acting, the ESS point remains quasi-periodic, with period varying about 6.0 over the range of parameters listed. However, if c_1 and c_2 are increased to 0.3, then for both single and double trade-offs the ESS point always lies in the stability region for the same parameter ranges. With further increase, to 0.5 in c_1 and c_2, the situation differs in just two respects. First, the ESS point is so positioned in the stability region that it can access the "exotic" large-amplitude periodic states that arise from the distortion of Arnol'd tongues (Greenman and Benton 2004). Second, for a single trade-off and low values of the trade-off constant σ_0 in equations (4) (but not too low for extinction to occur), the ESS attractor becomes a repeller, and the system evolves to the maximum limit ϕ_0 of ϕ in trade-offs of equations (4) and (7). In this case the species becomes semelparous, with $\sigma = 0$. If it is only adult and subadult populations that affect per capita reproduction (i.e., $c_1 = 0$, $c_2 \neq 0$), then the system response is different from the previous ($c_1 = c_2 \neq 0$) case in that, except for low values of ϕ or σ_0, the ESS remains quasi-periodic, with declining period as c_2 increases (table 1).

Discussion

We have shown that the ESS to which a single species evolves is oscillatory when described by a nonlinear matrix model with trade-offs between reproduction and survival and with density dependence, driven primarily by the adult stage, affecting only reproduction. The period of the oscillations lies in the range two to three times the time to maturation (MT), a result that appears to hold whatever the number of life-history stages included in the model.

How does this result compare with the empirical data on species periodicity? We have already referred to the data analyzed by Kendall et al. (1998). They present information on the dynamics of nearly 700 species. Of these, 29% were judged to exhibit cyclic patterns. Digitization of their data on the cycle periods (see fig. 1*b* of Kendall et al. 1998) indicates that the mean period is 7.8 years (median = 7.9, interquartile range = 5.1–9.6, range = 2–20, $n = 174$). All periods (in years) are represented up to 20, but with modes at 2, 4, and 6–10 years (table 2).

Table 2: Patterns of periodicity in cyclic populations

Data source, period	N
Kendall et al. 1998, fig. 1*b*:	
2	12
3	3
4	24
5	7
6	14
7	14
8	24
9	24
≥10	52
Murdoch et al. 2002:	
$0 < p \leq 2$	10
$2 < p \leq 4$	19
$4 < p \leq 6$	24
$6 < p \leq 8$	10
$8 < p \leq 10$	32
>10	1

Note: Period rounded to nearest integer. N = number of observations.

The bulk of Kendall's cycling species are mammals (109 populations), fish (56), birds (18), and insects (13). The mammals are mainly North American fur-bearing mammals, and the fish are typically harvested species. It is likely that the median age at maturation will be 1–3 years, making the median periodicity likely to be in the range (2–4)MT. A similar review by Murdoch et al. (2002) of 108 populations, from 40 species showing cyclic dynamics, finds a median cycle period of 6–8 years. To compare the empirical patterns with our model results, the cycle period in years must be scaled by the maturation time, which Murdoch et al. (2002) do. They find that 40 populations exhibit "single-generation cycles" (period $\simeq$ MT), 27 exhibit "delayed-feedback cycles" (periods in the range 2MT $\leq$ period $\leq$ 4MT), and 41 show "consumer resource cycles" (period > 4MT; table 2).

By studying the properties of a range of models, Gurney et al. (1983) and Gurney and Nisbet (1985) were able to relate the occurrence of these different types of behavior to differences in internal (density-dependent) structure. Cycling with period less than 2MT (typically "one-and-a-bit" MT) suggests the presence of density dependence of a form that directly changes the numbers in the affected stage (e.g., via changes in survival). Such cycles are referred to as "single-generation cycles" (SGCs). On the other hand, fluctuations with periods in the range 2MT $\leq$ period $\leq$ 4MT relate to density dependence with a delayed effect, for example, when current adult density affects juvenile numbers later (via changing fecundity). These cycles are called "delayed-feedback cycles" (DFCs). The period of the DFC is linked to the ratio of maturation time to adult life span: 4MT when adult survival is high, 2MT when it is low. Additionally, Nisbet and Onyiah (1994) showed that SGCs can arise when there are strong intercohort interactions (because these lead, via the "competitive exclusion" principle, to a single surviving cohort). Periods greater than 4MT are typically put down to consumer-resource interactions (e.g., see Murdoch et al. 2002). The stored product pest *Plodia* is an example of an immediate-effect system, with between-cohort interactions, leading to an SGC (Wearing et al. 2004). Nicholson's blowflies are an example of a delayed-effect system (competition affects size at maturity and fecundity). Forest Lepidoptera typically show outbreaks with a long cycle period (mean = 10.4 years, $n = 11$; Dwyer et al. 2004), which are often ascribed to consumer-resource dynamics, in this case predator-pathogen-host dynamics.

Analysis of ecological models has shown that whatever the density dependence structure, there is always a wide range of dynamical states from which the system can "choose." Why, then, do actual systems typically choose states that conform to the period structure rules that we have just discussed? The evolutionary answer is that actual systems are the ESSs of adaptive processes and that the rules are properties of the ESSs. This hypothesis is supported by our analysis of model (1) and its higher dimensional generalizations. This model is effectively a delayed-feedback model, in that density dependence affects fecundity and therefore the numbers in a later stage. This structure indicates an ESS with the characteristics of a DFC, that is, cycles with a period in the range (2–4)MT, the period being closer to 2MT when adult survival is low and increasing when adult survival is higher. This is what we found in our calculations (table 1, rows 1–3). The only situations when the ESS is either not cyclic or, if cyclic, has a period less than 2MT is when density dependence is a function not just of adults but also of subadults as well or, indeed, of all three stages. The cross-stage density dependence presumably creates a "blurring" of the cohort structure such that, on average, total population density, and hence fecundity, varies little from time step to time step. In the case where density dependence is a function of the two oldest age classes (table 1, rows 7–9), the cycle period decreases to below 2MT (the minimum in table 1 is 1.4MT). Such situations can be thought of as an example of asymmetric intercohort competition, with the density of large animals suppressing the density of the smallest animals, leading to cycles that approach SGCs (Nisbet and Onyiah 1994; Knell 1998).

Our calculations are therefore in line with observed patterns of periodicity, but they do not provide us with much understanding of why these particular states should be chosen by the evolutionary process out of the multiplicity of states that are available. Why, for example, should a

single-species system with delayed density dependence lead to an ESS with period in the range (2–4)MT? However, we can gain some insight by refocusing on the properties of the ESS itself. By definition, at an ESS alternative strategies cannot invade the resident; in our case, an alternative strategy is one with a different value on the trade-off curve(s). Changing the position of the trade-off creates a change in survival and fecundity and hence in the dynamics. At the ESS, typically there will be alternation of low- and high-density cohorts: adults at high density lay few eggs, which mature into a low-density cohort, laying many eggs. In a high-density cohort, increasing fecundity may have little advantage because fecundity is minimal as a result of density, and decreasing fecundity (to increase survival) may result in reproductive output too low to allow surviving offspring. In a low-density cohort, increasing fecundity may lead to little advantage, as it will lead to greater numbers of juveniles, which, when they mature, suffer decreased fecundity.

Taking a different approach, we can gain additional insight into the periodicity structure of ESSs by looking at the geometry of the stability region for the system (fig. 2). First we note that there is a gap in the (eigenvalue) periods associated with the points on the boundary of this region. On the quasi-periodic boundary, the periods range from 2MT to *s*MT (where $s = 2/3$ when MT is even and 1 when MT is odd) and 2MT to infinity. On the other boundaries, the periods are constant at 2 and infinity. There is therefore a gap in the range of boundary periods, from *s*MT to 2MT, starting and ending at corners of the stability region. A system with delayed density dependence evolving through a sequence of oscillatory states with diminishing period close to the quasi-periodic boundary will therefore eventually experience a barrier in period at 2MT. The ESS point lies close to the corner where this barrier is reached. (It should be noted that the period jump and gap properties are properties of systems with at least three life-history stages and therefore have no effect in two-dimensional juvenile-adult models.)

With the ESS point near the boundary of the stability region, the system is highly sensitive to noise (Greenman and Benton 2003). Being near the quasi-periodic boundary, the period of the population oscillations is highly sensitive to parameter values. Small changes in values lead to significant changes in period. This is also the region in which there can be multiple periodic attractors. Near a corner of the quasi-periodic boundary, there is more than one real eigenvalue or complex conjugate pair of eigenvalues that are simultaneously close to dominance and hence to more attractors that are accessible. For the 3×3 LPA model (Cushing et al. 1998), for example, oscillations of both periods 6 and 2 can be excited from the ESS by noise or appropriate choice of initial conditions.

The sensitivity of periodicity to parameter values has important consequences: slightly different life histories might have similar "fitness," especially in a stochastic environment (Orzack 1993), but could cycle with appreciably different periods, and the strength of selection may mean that the approach to the ESS is slow. Habitat change may also result in small changes in biological parameters, leading to a marked change in cycle period. Variation in cycle period with variation in environmental conditions is known for several species, such as red grouse (Haydon et al. 2002) and rodents (Stenseth 1999).

There is a body of opinion that ecological systems evolve toward the "edge of chaos," either deterministic chaos or stochastic chaos (Ellner and Turchin 1995; Bourgine and Snyers 1996; Ellner et al. 1998; Turchin and Ellner 2000; de Oliveira 2001; Sole et al. 2002; Greenman and Benton 2003). Stochastic chaos describes behavior at a system threshold where the system is highly responsive to stochastic forces and highly sensitive to initial conditions; that is, it is "chaotic," at least in the short term (Greenman and Benton 2003). Model (1) is consistent with the edge-of-chaos hypothesis, although the ESS is not arrived at through group selection, which is often an implicit assumption of the edge-of-chaos arguments.

There has been recent discussion about the causes of population fluctuations and whether from single-species time series one could infer the causation of particular periodicities (Murdoch et al. 2002; Wearing et al. 2004). As Wearing et al. (2004) have noted, different mechanisms (e.g., consumer resource dynamics or cohort competition) can give rise to the same periods, and the same mechanisms can give rise to different periods (as we show here). Inferring causation from the periodicity of the time series alone may be problematic. This is perhaps emphasized by recent studies of red grouse dynamics. Haydon et al. (2002) show 63.3% of 289 time series for red grouse to be either strongly or weakly cyclic (with periodicity of 3.5–13 years, min − max, and a mean of 8.3 years for strongly cyclic series and 7.1 years for weakly cyclic series). With $MT = 1$ year, the lower end of the range would fall into the expected dynamics created by delayed-feedback models, and the upper end would fall into periodicities expected by consumer resource dynamics (Murdoch et al. 2002). However, Shaw et al. (2004) suggest that there is little evidence from the time series for different biological causation for changes in cycle period.

Finally, we note that investigation of the evolutionary dynamics of populations is of applied as well as theoretical importance, given the number of instances in which life-history evolution is being recorded over "ecological" time scales (Fussmann et al. 2003; Stockwell et al. 2003; Turchin 2003; Yoshida et al. 2003; Olsen et al. 2004). Population dynamics should not treat the underlying parameters as

constants, given the potential for them to evolve, and this is perhaps especially true where population management is concerned (Ashley et al. 2003; Stockwell et al. 2003). Our analysis illustrates the adaptive dynamics trade-off approach to parameter evolution in the special but important situation where a species exhibits intrinsically generated periodic oscillations.

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APPENDIX

Sample Mathematica code to construct the stability region, to simulate the system, and to calculate the leading Lyapunov exponent can be found in the online edition of the *American Naturalist.*[1]

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[1] The Mathematica notebook is being archived as sample code. The code has not been peer-reviewed, and neither the journal nor the authors are able to provide support.

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