Evolutionary Ecology Research, 2006, **8**: 387–398

Evolutionary behaviour in ecological systems with trade-offs and non-equilibrium population dynamics

A. White,[1]* J.V. Greenman,[2] T.G. Benton[3] and M. Boots[4]

[1]*Department of Mathematics, School of Mathematical and Computer Sciences, Heriot Watt University, Edinburgh EH14 4AS,* [2]*Department of Computing Science and Mathematics, University of Stirling, Stirling FK9 4LA,* [3]*Earth and Biosphere Institute, School of Biology, University of Leeds, Leeds LS2 9JT and* [4]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

ABSTRACT

Question: Do non-equilibrium (cycles or chaos) population dynamics change evolutionary behaviour when compared with equilibrium dynamics?

Mathematical methods: The theory of adaptive dynamics is applied to a discrete ecological model with an explicit trade-off between reproduction and survival. Simulation techniques are compared with the theoretical findings.

Key assumptions: Mutations in life-history parameters are assumed to be small. A separation of the ecological and evolutionary time scales is assumed. There is a feedback loop between the environment and its inhabitants.

Conclusions: With equilibrium population dynamics the shape of the trade-off can be used to characterize the evolutionary behaviour. Trade-offs with accelerating costs produce a continuously stable strategy (CSS). Trade-offs with decelerating costs produce a non-evolutionarily stable strategy (non-ESS) repellor. The characterization holds for non-equilibrium dynamics with low amplitude population oscillations. When the magnitude of the population oscillation exceeds a threshold, the characterization fails. Trade-offs with decelerating costs can produce a CSS, multiple CSSs or evolutionary branching points. The evolution of reproduction and survival parameters may be contingent on initial conditions and sensitive to small changes in other life-history parameters. Evolutionary branching allows types with distinct reproduction and survival parameters to evolve and co-exist.

Keywords: adaptive dynamics, evolutionary branching in fecundity, population oscillations, trade-offs.

INTRODUCTION

The evolution of life-history traits, such as reproduction and survival, is fundamental to individual fitness and therefore for explaining the diversity and complexity of natural systems (Stearns, 1992). Central to life-history evolutionary theory is the role of trade-offs

---

* Author to whom all correspondence should be addressed. e-mail: a.r.white@hw.ac.uk

between life-history traits. These arise when the evolution of particular fitness traits are constrained by negative correlations with other life-history traits such that a benefit in one character results in a cost in another (Stearns, 1992; Roff, 2002). It is widely recognized that the shape of the trade-off between life-history parameters is important in determining the evolutionary behaviour of a system. This is true in the context of classical life-history theory (Levins, 1962; Schaffer, 1974; Stearns, 1992; Roff, 2002) and in more recent studies that use adaptive dynamics to assess the evolutionary behaviour of ecological systems (Boots and Haraguchi, 1999; Kisdi, 2001; Bowers *et al.*, 2003; de Mazancourt and Dieckmann, 2004; White and Bowers, 2005). Furthermore, the importance of the trade-off shape in characterizing evolutionary behaviour has recently been recognized with the development of general geometric methods for analysing the adaptive dynamics of ecological systems (de Mazancourt and Dieckmann, 2004; Rueffler *et al.*, 2004; Bowers *et al.*, 2005).

Most theoretical studies of the evolution of life-history traits have assumed equilibrium underlying population dynamics. It is known that ecological systems can exhibit a range of complicated population dynamics, such as periodic and quasi-periodic cycles and chaos (see Katok and Hasselblatt, 1998), and that simple models can capture this complicated behaviour (Gurney and Nisbet, 1998; Cushing *et al.*, 2003). It is therefore important to assess how the underlying population dynamics affect evolutionary behaviour. A large body of work on the evolution of life-history parameters has tried to determine whether evolution leads to equilibrium or non-equilibrium dynamics (Gatto, 1993; Ferriere and Gatto, 1993; Doebeli and Koella, 1995; Ebenman *et al.*, 1996; Greenman *et al.*, 2005). In addition, the evolution of dispersal rates has been considered for non-equilibrium dynamics (Doebeli and Ruxton, 1997; Parvinen, 1999). Clearly, these studies have investigated evolution in non-equilibrium environments. However, they have not considered how the trade-off shape between life-history parameters interacts with the underlying population dynamics to affect the evolutionary behaviour. We wish to examine whether changes in the population dynamics can change the evolutionary behaviour expected for fixed shapes of trade-offs. To achieve this we will analyse a simple, discrete model that can exhibit equilibrium and non-equilibrium population dynamics. We will explicitly define a trade-off between reproduction and survival and investigate how the underlying population dynamics affect the outcome of evolution.

METHODS

We develop a discrete time model with an explicit trade-off between reproduction and survival. Such a model is chosen not only for its biological simplicity and therefore reasonable generality, but also because it can exhibit a range of complex behaviours.

The model considers the reproduction and survival of a single species with density X, and includes density-dependent regulation that acts through reproduction. The model is described as follows:

$$X_{t+1} = \phi X_t \exp(-X_t) + \sigma X_t \tag{1}$$

Here, ϕ is the per capita number of births per generation and σ ($\in [0,1)$) is the proportional survival per generation. This system has a trivial equilibrium at the origin and equilibrium at $\hat{X}$ where

$$\hat{X} = \ln\left(\frac{\phi}{1-\sigma}\right) \tag{2}$$

The equilibrium is stable whenever it is positive provided that

$$(1-\sigma)\ln\left(\frac{\phi}{1-\sigma}\right) < 2 \tag{3}$$

When inequality (3) is not satisfied, the equilibrium becomes unstable and the system exhibits periodic cycles or chaos depending on the precise values of the parameters.

A general trade-off formulation is used to examine the relationship between the shape of the trade-off and the evolutionary behaviour predicted by the theory and simulations. Throughout the analysis in this study, we will assume that there is a trade-off between fecundity and survival such that $\sigma = f(\phi)$ [where $f'(\phi) < 0$ so that an increase in ϕ is bought at a cost of a decrease in σ]. The formulation is defined as:

$$\sigma = f(\phi) = \sigma_{\min} + \frac{(\sigma_{\max} - \sigma_{\min})\left(1 - \dfrac{(\phi - \phi_{\min})}{(\phi_{\max} - \phi_{\min})}\right)}{\left(1 + a\dfrac{(\phi - \phi_{\min})}{(\phi_{\max} - \phi_{\min})}\right)} \tag{4}$$

The curvature of the trade-off can then be altered by varying a (Fig. 1). If $-1 < a < 0$, then $f''(\phi) < 0$ and the trade-off has accelerating costs. If $a > 0$, then $f''(\phi) > 0$ and the trade-off has decelerating costs.

The theoretical analysis uses the theory of adaptive dynamics (Metz *et al.*, 1996; Geritz *et al.*, 1998). We will apply the theory to this study by assuming that a resident type, with parameter ϕ (and therefore also $\sigma = f(\phi)$) has dynamics represented by equation (1) and has reached its attractor (which could be an equilibrium point or a more complicated attractor). The theory of adaptive dynamics assesses whether a mutant type represented by the same dynamics but with a different parameter $\tilde{\phi}$ (and $\tilde{\sigma} = f(\tilde{\phi})$) could invade, co-exist with or oust the

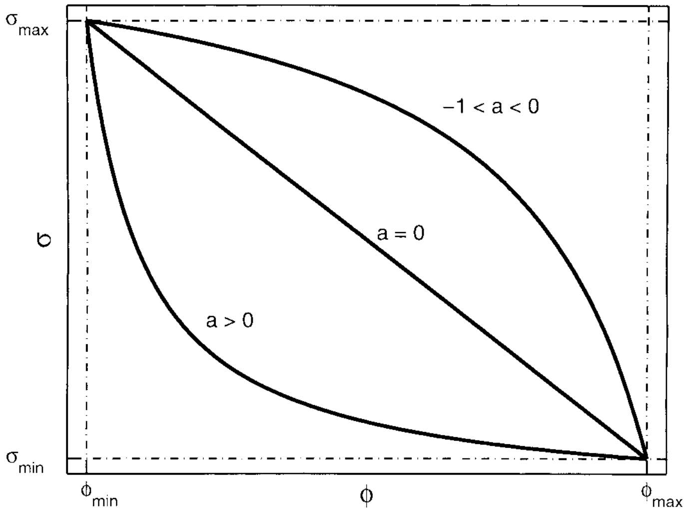

Fig. 1. The generalized trade-off as described by equation (4). The trade-off has accelerating costs if $-1 < a < 0$ and decelerating costs if $a > 0$.

established resident type. It is assumed that there is a small but distinct difference between mutant and resident parameters and that the mutant is initially at low density. The key term to determine the fate of the mutant is the fitness of the mutant type [calculated as the per capita growth rate of the mutant – which equates to the largest Lyapunov exponent (Metz *et al.*, 1992)] in the environment set by the resident, which is denoted $s(\tilde{\phi}, \phi)$. If this is negative the mutant cannot invade and dies out. If it is positive the mutant can invade, increase its density and could co-exist with or oust the resident to become the resident itself, thereby reshaping the resident environment. Given that mutations are small, the population will evolve in the direction of the local fitness gradient, defined as $[\partial s(\tilde{\phi}, \phi)/\partial\tilde{\phi}]_{\phi = \tilde{\phi}}$ until it reaches a singular strategy, ϕ^*, for which the fitness gradient is zero. The behaviour at the singular strategy is determined by the topology of the fitness surface at the singular point and is characterized by combinations of the associated second-order partial derivatives of the fitness function with respect to the mutant and resident strategies (Table 1). For instance, if ϕ^* is not convergence stable and not an evolutionarily stable strategy (ESS), it is a non-ESS repellor (Metz *et al.*, 1996), whereas if it is not convergence stable but is an ESS, it exhibits 'Garden of Eden' evolutionary behaviour (Nowak, 1990). If ϕ^* is convergence stable and an ESS, it is a continuously stable strategy (CSS) (Metz *et al.*, 1996; Geritz *et al.*, 1998). The phenomenon of branching occurs when ϕ^* is convergence stable but not an ESS. Here we evolve towards ϕ^* but when close by undergo disruptive selection, which results in the co-existence of two distinct strategies. [See Metz *et al.* (1996) and Geritz *et al.* (1998) for more details on the theory of adaptive dynamics.]

Simulation analysis is used to verify the theoretical results about the position and nature of the singular strategy. In the simulations, the population dynamics were numerically solved for a fixed time (t_a) according to equation (1) initially with a monomorphic population. Mutant strategies were generated by small deviations around the current strategies (the choice of current strategy from which to mutate depends on its relative density) and introduced at low density. The population dynamics were then solved for a further time t_a with strategies whose population density fell below a (low) threshold considered extinct and removed before considering new mutations. In this way, the parameter ϕ (and therefore σ via the trade-off) could evolve. One difference between the theory and simulations is that the simulations are not mutation-limited (i.e. new mutants could evolve before previous mutants had reached equilibrium or gone extinct). However, this set-up has been shown to correctly approximate the evolutionary behaviour predicted by adaptive dynamics in studies where the dynamical attractor is an equilibrium point (see, for example, Kisdi, 1999; White and Bowers, 2005).

Table 1. Properties of the singular strategy, ϕ^* (see Geritz *et al.*, 1998)

Property	Characteristic
Evolutionarily stable strategy (ESS)	$B < 0$
Convergence stable	$A - B > 0$
$A = \left.\dfrac{\partial^2 s(\tilde{\phi}, \phi)}{\partial \phi^2}\right\|_{\tilde{\phi} = \phi = \phi^*}$ $\quad B = \left.\dfrac{\partial^2 s(\tilde{\phi}, \phi)}{\partial \tilde{\phi}^2}\right\|_{\tilde{\phi} = \phi = \phi^*}$	

RESULTS

Equilibrium underlying population dynamics

When the resident population exhibits stable equilibrium dynamics, the fitness of the mutant strategy is described as follows:

$$s(\tilde{\phi}, \phi) = \tilde{\phi}\, e^{-\hat{X}} - [1 - f(\tilde{\phi})] \tag{5}$$

Here, $\hat{X}$ denotes the equilibrium density of the resident (defined by (2)) and therefore contains resident parameters.

We apply the theory of adaptive dynamics to equation (5). The singular strategy, ϕ^*, occurs when $[\partial s(\tilde{\phi}, \phi)/\partial\tilde{\phi}]_{\phi=\tilde{\phi}}$ is zero, which occurs when

$$f'(\phi^*) = \frac{f(\phi^*) - 1}{\phi^*} \tag{6}$$

The behaviour at the singular strategy is determined from combinations of the associated second-order partial derivatives of the fitness function with respect to the mutant and resident strategies and can be characterized by two properties (Table 1). For the dynamics represented by system (1), at the singular point $\phi = \tilde{\phi} = \phi^*$, we find

$$\frac{\partial^2 s(\tilde{\phi}, \phi)}{\partial\tilde{\phi}^2} = \frac{f''(\phi^*)}{1 - f(\phi^*)} \quad \text{and} \quad \frac{\partial^2 s(\tilde{\phi}, \phi)}{\partial\phi^2} = \frac{-f''(\phi^*)}{1 - f(\phi^*)} \tag{7}$$

Thus in terms of the results outlined in Table 1, we can see that $A = -B$. Hence when $f''(\phi^*) < 0$ (a trade-off with $-1 < a < 0$; Fig. 1), the singularity is an ESS, is necessarily convergence stable and therefore a CSS. When $f''(\phi^*) > 0$ (a trade-off with $a > 0$; Fig. 1), the singularity is not an ESS and not convergence stable and is therefore a non-ESS repellor (see White and Bowers, 2005). Figure 2a shows the position of the singular strategy as determined by (6) and the final evolved values of ϕ from simulations for different values of the curvature of the trade-off. When $-1 < a < 0$, the singular strategy is a CSS and the theoretical and simulation results are in agreement. When $a > 0$, the singular strategy is a non-ESS repellor and ϕ evolves to the maximum value in simulations (it is repelled away from the singular point as expected). Thus with equilibrium underlying dynamics, the evolutionary behaviour of the model (equation 1) can be partitioned depending on whether the trade-off has accelerating or decelerating costs. We note here that the model supports an optimization principle (Mylius and Diekmann, 1995). The equilibrium density of the resident type could be included explicitly in equation (5) and therefore the optimal strategy will be the type that maximizes $\phi/[1 - f(\phi)]$. This rules out the possibility of co-existence and evolutionary branching.

Non-equilibrium underlying population dynamics

It is rarely possible to determine the largest Lyapunov exponent (fitness) algebraically when the underlying dynamics are non-equilibrium. It is possible, however, to compute the largest Lyapunov exponent numerically (Eckmann and Ruelle, 1985; Metz *et al.*, 1992; Ferriere and Gatto, 1993). For the model system (1), the largest Lyapunov exponent – and therefore the fitness of the mutant strategy – is defined as

$$s(\tilde{\phi}, \phi) = \lim_{t\to\infty} \frac{1}{t} \ln(M_{t-1} \cdot M_{t-2} \cdot \ldots \cdot M_1 \cdot M_0) \tag{8}$$

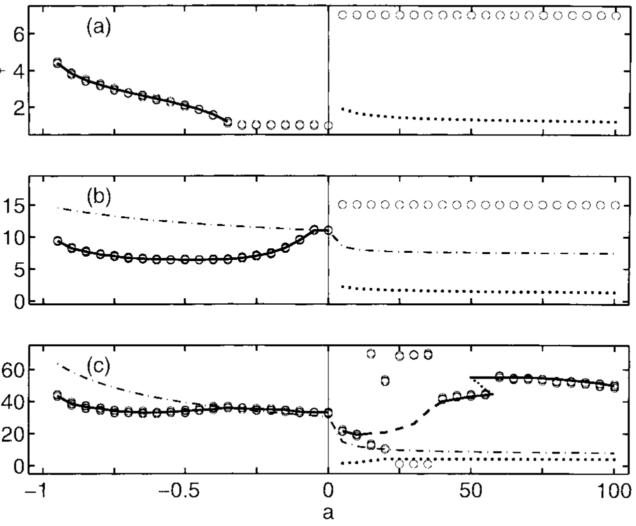

Fig. 2. The theoretical value of the singular strategy ϕ^* and simulation predictions for the final evolving values of ϕ (open circles) for different trade-off shapes. For the theoretical results, a CSS is denoted by a solid black line, a non-ESS repellor by a dotted line and an evolutionary branching point by a dashed line. The dash-dot line indicates where the population dynamics are equilibrium (below) and non-equilibrium (above). The trade-off parameters are $\phi_{\min} = 1$, $\sigma_{\min} = 0$, $\sigma_{\max} = 0.9$. In (a) $\phi_{\max} = 7$, which produces equilibrium population dynamics for all possible parameter values. In (b) $\phi_{\max} = 15$ and (c) $\phi_{\max} = 70$ and here the population dynamics change from equilibrium to non-equilibrium (periodic cycles and chaos) as ϕ increases on the trade-off. For all simulations, the initial conditions assumed that $\phi = (\phi_{\max} - \phi_{\min})/2$ was the only population type with positive density.

where $M_{t-1} = \tilde{\phi} e^{-X_{t-1}} + \tilde{\sigma}$, and X_{t-1} are the successive population values of X for the resident strategy on its attractor (for further details, see Eckmann and Ruelle, 1985; Metz *et al.*, 1992; Ferriere and Gatto, 1993). The values of $s(\tilde{\phi}, \phi)$ for different resident–mutant combinations can be used to determine the sign structure of the fitness expression and to construct pair-wise invadability plots (Metz *et al.*, 1992; Geritz *et al.*, 1998; and see Figs. 4 and 5), which can be used to infer the positions of the singular strategies and their evolutionary behaviour (and are referred to as the theoretical results below).

Figures 2b and 2c show results when the parameters that specify the trade-off are chosen such that the underlying dynamics change from equilibrium to non-equilibrium as ϕ increases along the trade-off. In Fig. 2b, the qualitative results are similar to those for equilibrium dynamics (Fig. 2a). Here the shape of the trade-off curve can still be used to partition the evolutionary behaviour. In Fig. 2c, this partitioning no longer applies. A CSS is still predicted for a trade-off with accelerating costs, but the evolutionary behaviour is more complicated for a trade-off with decelerating costs. (Note, it is possible to specify a trade-off that exhibits non-equilibrium dynamics for all parameter combinations. The results are qualitatively similar to those in Figs. 2b and 2c.) For a trade-off with decelerating costs, the non-ESS repellor remains for values of ϕ near $\phi_{\min}$ but other singular points are also predicted such that for some values of a we observe a CSS, multiple CSSs or evolutionary branching points. To understand how this evolutionary behaviour occurs, we fix $a = 20$ and increase $\phi_{\max}$ (Fig. 3). As $\phi_{\max}$ increases beyond $\phi_{\max} = 20$, a CSS occurs just below $\phi_{\max}$

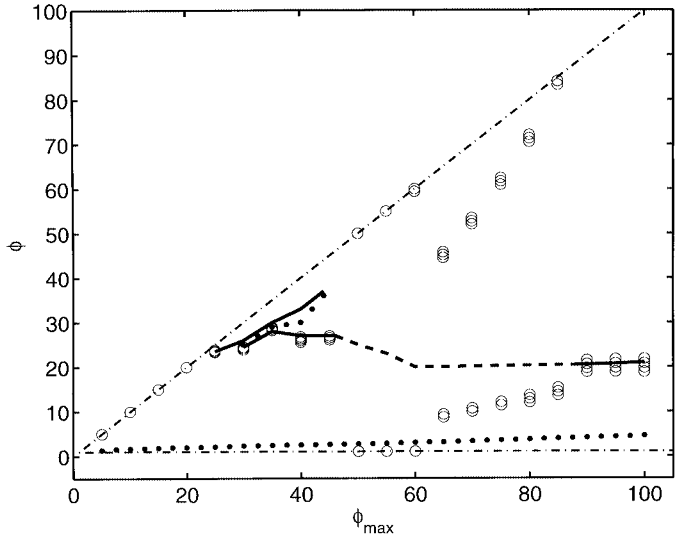

Fig. 3. The theoretical value of the singular strategy ϕ^* and simulation predictions for the final evolved value of ϕ (open circles) for different values of ϕ_{max}. For the theoretical results, a CSS is denoted by a solid black line, a non-ESS repellor by a dotted line and an evolutionary branching point by a dashed line. The trade-off parameters are $\phi_{min} = 1$, $\sigma_{min} = 0$, $\sigma_{max} = 0.9$ and $a = 20$. The dash-dot lines indicate the value of ϕ_{min} and ϕ_{max}. For all simulations, the initial conditions assumed that $\phi = (\phi_{max} - \phi_{min})/2$ was the only population type with positive density.

(note that the non-ESS repellor is still present at ϕ near ϕ_{min} throughout). This can be visualized clearly in a pair-wise invadability plot, which shows how the fitness landscape bends upwards and a CSS emerges from ϕ_{max} (Figs. 4a and 4c). The population dynamics at the final evolved value of ϕ shows how the amplitude of oscillations increases as ϕ_{max} increases (Figs. 4b and 4d). In the Discussion, we explain how this increase in the amplitude of oscillations could be responsible for the change in evolutionary behaviour that allows a CSS to form. As ϕ_{max} is increased further, two CSSs are observed, separated by a non-ESS repellor; these then become a single CSS once more, then a branching point and finally a CSS (Fig. 3). An understanding of this behaviour can be gained by examining pair-wise invadability plots as these transformations occur (Fig. 5). At $\phi_{max} = 30$ (Fig. 5a), a 'fold' in the line on which $s(\tilde{\phi}, \phi) = 0$ creates two CSSs separated by a non-ESS repellor. As ϕ_{max} increases, this fold increases in size (Fig. 5b) but by $\phi_{max} = 45$ one branch of the fold lies below the line $\tilde{\phi} = \phi$, leaving only one CSS (Fig. 5c). At $\phi_{max} = 50$, the fitness landscape reconfigures transforming the CSS into a branching point (Fig. 5d). Further increases in ϕ_{max} transform the branching point into a CSS (at approximately $\phi_{max} = 85$; see Figs. 5e and 5f). These results highlight how non-equilibrium population dynamics can dramatically change the fitness landscape.

DISCUSSION

This study has examined how evolutionary behaviour may be affected when the underlying population dynamics change from stable equilibrium to non-equilibrium (cycles or chaos).

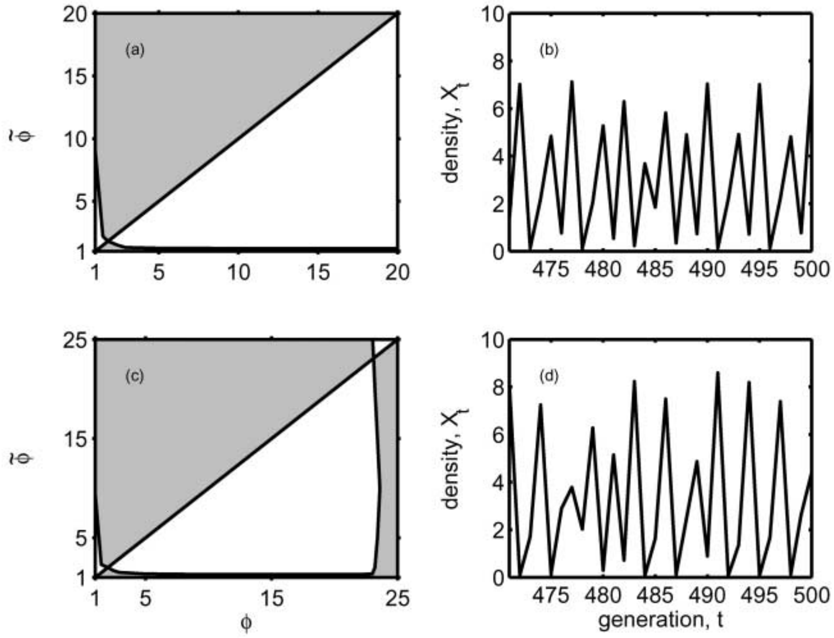

Fig. 4. (a, c) Pair-wise invadability plots with regions of positive fitness in grey and negative fitness in white. (b, d) The underlying population dynamics for the evolved value of ϕ from the simulations. The trade-off parameters are $\phi_{\min} = 1$, $\sigma_{\min} = 0$, $\sigma_{\max} = 0.9$, $a = 20$. In (a) and (b), $\phi_{\max} = 20$ and the evolved value of $\phi = 20$. In (c) and (d), $\phi_{\max} = 25$ and the evolved value of $\phi = 23$.

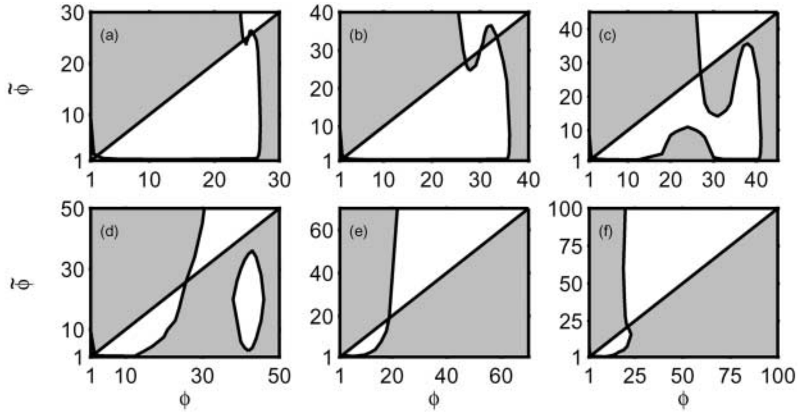

Fig. 5. Pair-wise invadability plots with regions of positive fitness in grey and negative fitness in white. The trade-off parameters are $\phi_{\min} = 1$, $\sigma_{\min} = 0$, $\sigma_{\max} = 0.9$, $a = 20$. In (a) $\phi_{\max} = 30$, (b) $\phi_{\max} = 40$, (c) $\phi_{\max} = 45$, (d) $\phi_{\max} = 50$, (e) $\phi_{\max} = 70$ and (f) $\phi_{\max} = 100$.

The evolutionary behaviour for the model (equation 1), with underlying equilibrium dynamics, could be characterized by the trade-off cost structure. In this case, a trade-off with accelerating costs would produce a CSS and one with decelerating costs a non-ESS repellor. This is equivalent to the findings of previous studies using adaptive dynamics to examine ecological models that exhibit an optimization principle (Bowers *et al.*, 2003; White and Bowers, 2005). For models that do not exhibit an optimization principle, a broader range of evolutionary behaviour is possible. For example, a trade-off with weakly decelerating costs may exhibit evolutionary branching (Boots and Haraguchi, 1999; Kisdi, 2001; Bowers *et al.*, 2003; White and Bowers, 2005), whereas one with weakly accelerating costs may exhibit a Garden of Eden strategy (White and Bowers, 2005). These studies emphasize the need for a more detailed understanding of how ecological interactions combine with trade-off shape to produce different types of ecological behaviour. This analysis will be assisted by the recent development of geometric methods for analysing the adaptive dynamics of ecological systems with trade-offs (de Mazancourt and Dieckmann, 2004; Rueffler *et al.*, 2004; Bowers *et al.*, 2005). The present study, however, focuses on how changes in the underlying population dynamics could affect the evolutionary behaviour.

When the population dynamics were non-equilibrium with small population oscillations, the evolutionary behaviour could be characterized by trade-off shape in a corresponding manner to equilibrium dynamics (Figs. 2a and 2b). However, when the parameter choice resulted in non-equilibrium population dynamics with large oscillations, new evolutionary singular points emerged and a range of evolutionary behaviour could be observed (in addition to the non-ESS repellor behaviour). When the amplitude of the population oscillations exceeded a threshold, a new singular strategy emerged (Fig. 4). The population oscillations result from overcompensating density dependence and we believe it is this that causes the difference in evolutionary behaviour when compared with the behaviour for equilibrium or low oscillation underlying dynamics. Intuitively, the effect of overcompensating density dependence can be understood as follows. When population numbers are low, a high birth rate is advantageous (since density-dependent effects are small), but as adult numbers increase (which occurs when population oscillations exceed a threshold), the benefit from a high birth rate is diminished since the density-dependent effects are overcompensating (high population numbers produce a low number of births). However, a higher birth rate equates to a lower survival rate through the trade-off. The survival rate is not affected by density dependence. Thus the full benefit of a high birth rate is not realized but the full cost in terms of reduced survival is. Thus evolution to maximum values of ϕ is no longer favoured. If this intuitive argument is to be believed, it must apply in other systems with overcompensating density dependence and a trade-off between birth and survival. The same phenomenon has been shown to occur if the model (equation 1) is extended to include age structure, and in different model systems such as the larvae–pupae–adult model (Cushing *et al.*, 2003) and the Neubert-Caswell reproduction model (Neubert and Caswell, 2000). The requirement is that the underlying dynamics are non-equilibrium with population oscillations exceeding a threshold. It is also expected that this phenomenon would hold in continuous systems in which overcompensating density dependence could produce large oscillations (for example, in systems that include an explicit time delay) and may also arise in systems where stochastic variation produces sufficiently large population fluctuations.

The trade-off between fecundity and survival considered in this study is a life-history trade-off reflected by internal competition for resources within individuals. Density dependence can act as a form of 'external trade-off', driven by competition for resources between individuals – the greater an individual's fecundity, the more competition it (or its offspring) will face in the future, thereby reducing survival. As argued above, this can act as a break on the evolution of fecundity. It is therefore important to determine how the cost structure of density dependence affects the outcome of evolution. In the present study, the density dependence term [exp(− X)] has decelerating costs as population numbers increase. By replacing this density dependence term by the theta logistic term $[1 - (Z/K)^{\theta}]$, we can assess how density dependence with accelerating costs ($\theta > 1$) and decelerating costs ($\theta < 1$) affects evolutionary behaviour. This is important, as there is evidence to suggest that many invertebrates tend to show density dependence with decelerating costs, while vertebrates characteristically show density dependence with accelerating costs (Sibly and Hone, 2002). We repeated the analysis in this study for different shapes of the density dependence trade-offs (results not shown here) and found qualitatively similar results regardless of the shape of the density dependence in the trade-off. In particular, when the amplitude of the population oscillations passes a threshold, an additional evolutionary singular strategy emerges (as in Fig. 4). This adds further strength to the argument that it is the large oscillations that produce the change in evolutionary behaviour.

In addition to the emergence of a new evolutionarily singular strategy, a wide range of evolutionary behaviour is possible as the amplitude of population oscillations increases. Folds in the fitness landscape can result in two CSSs separated by a non-ESS repellor (Figs. 2c, 3, 5a and 5b). Here the end-point of evolution is contingent on initial conditions (i.e. on which side of the fold the initial type lies). Also, small changes in the value of $\phi_{\mathbf{max}}$ or a can mean part of the fold no longer intersects with the line $\phi = \tilde{\phi}$ (compare Figs. 5b and 5c). Therefore, small changes in life-history parameters can make a CSS ‘disappear’. This could result in large shifts in the value of the evolving parameters. A further novel result is that of evolutionary branching in fecundity (Figs. 2c, 3, 5d and 5e). This occurs for a wide range of parameters, provided that the threshold in the amplitude of population oscillations has been surpassed and results in the co-existence of two types, typically one with high and one with low fecundity.

The results of the present study can be used to examine an important question in life-history theory on the evolution of reproductive effort. This question was first posed by Cole (1954), who examined whether populations evolve semelparous (reproduce only once) or iteroparous (reproduce more than once) reproductive strategies. In the context of our study, semelparity implies maximum reproductive effort (and therefore minimum survival). Many models have been developed to examine this (for an overview, see Stearns, 1992; Roff, 2002) and indicate that for equilibrium underlying dynamics, a trade-off with accelerating costs would promote intermediate reproductive effort (iteroparity), whereas a trade-off with decelerating costs would promote maximal reproductive effort. The results of our study confirm these findings when the underlying dynamics are equilibrium or have low amplitude oscillations. Studies have also examined the evolution of reproductive effort in non-equilibrium environments that result from the inclusion of environmental variation (Bulmer, 1985; Orzack and Tuljapurkar, 1989; Benton and Grant, 1999; Ranta *et al.*, 2002), variation in population dynamics (Ranta *et al.*, 2000a) and spatial structure (Ranta *et al.*, 2000b). These studies have shown that environmental variation selects for increased reproductive life span and iteroparity can replace or co-exist with semelparity (see Stearns, 1992). This is because the semelparous individuals invest all their reproductive effort in one generation, even if the environment is ‘poor’. By spreading reproduction over several time-steps, the iteroparous strategy can mitigate the effects of ‘poor’ environments and ensure it has surviving offspring when the environment becomes more favourable. Our study has confirmed these findings and emphasizes that population fluctuations may need to be large for an iteroparous type to invade (Orzack and Tuljapurkar, 1989). Our study also shows that population fluctuations can lead to the co-existence of types with distinct reproductive strategies through a process of evolutionary branching in fecundity. Evolutionary branching has been proposed as a possible mechanism for sympatric speciation and in this study requires a trade-off between reproduction and survival with decelerating costs and population fluctuations.

In summary, we have shown how the underlying population dynamics can have a marked effect on the evolutionary behaviour exhibited for different trade-off cost structures. In particular, a range of evolutionary behaviour can be exhibited for non-equilibrium population dynamics. This has important consequences, since many natural systems exhibit non-equilibrium dynamics.

ACKNOWLEDGEMENTS

We are grateful for discussions with Professor Jonathan Sherratt and for the suggestions and guidance of Dr Eva Kisdi.

REFERENCES

Benton, T.G. and Grant, A. 1999. Optimal reproductive effort in stochastic, density-dependent environments. *Evolution*, **53**: 677–688.

Boots, M. and Haraguchi, Y. 1999. The evolution of costly resistance in host–parasite systems. *Am. Nat.*, **153**: 359–370.

Bowers, R.G., White, A., Boots, M., Geritz, S.A.H. and Kisdi, E. 2003. Evolutionary branching/speciation: contrasting results from systems with explicit or emergent carrying capacities. *Evol. Ecol. Res.*, **5**: 883–891.

Bowers, R.G., Hoyle, A., White, A. and Boots, M. 2005. The geometric theory of adaptive evolution: trade-off and invasion plots. *J. Theor. Biol.*, **233**: 363–377.

Bulmer, M.G. 1985. Selection of iteroparity in a variable environment. *Am. Nat.*, **126**: 63–71.

Cole, L.C. 1954. The population consequences of life history phenomena. *Quart. Rev. Biol.*, **29**: 103–137.

Cushing, J.M., Costantino, R.F., Dennis, B., Desharnais, R.A. and Henson, S.M. 2003. *Chaos in Ecology*. London: Academic Press.

de Mazancourt, C. and Dieckmann, U. 2004. Trade-off geometries and frequency-dependent selection. *Am. Nat.*, **164**: 765–778.

Doebeli, M. and Koella, J.C. 1995. Evolution of simple population dynamics. *Proc. R. Soc. Lond. B*, **260**: 119–125.

Doebeli, M. and Ruxton, G.D. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution*, **51**: 1730–1741.

Ebenman, B., Johansson, A., Jonsson, T. and Wennergren, U. 1996. Evolution of stable population dynamics through natural selection. *Proc. R. Soc. Lond. B*, **263**: 1145–1151.

Eckmann, J.-P. and Ruelle, D. 1985. Ergodic theory of chaos and strange attractors. *Rev. Mod. Phys.*, **57**: 617–656.

Ferriere, R. and Gatto, M. 1993. Chaotic population dynamics can result from natural selection. *Proc. R. Soc. Lond. B*, **251**: 33–38.

Gatto, M. 1993. The evolutionary optimality of oscillatory and chaotic dynamics in simple population models. *Theor. Pop. Biol.*, **43**: 310–336.

Geritz, S.A.H., Kisdi, E., Meszéna, G. and Metz, J.A.J. 1998. Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.

Greenman, J.V., Benton, T.G., Boots, M. and White, A. 2005. The evolution of population dynamics in age-structured populations. *Am. Nat.*, **166**: 68–78.

Gurney, W.S.C. and Nisbet, R.M. 1998. *Ecological Dynamics*. Oxford: Oxford University Press.

Katok, A. and Hasselblatt, B. (1998). *Introduction to the Modern Theory of Dynamics Systems*. Cambridge: Cambridge University Press.

Kisdi, E. 1999. Evolutionary branching under asymmetric competition. *J. Theor. Biol.*, **197**: 149–162.

Kisdi, E. 2001. Long-term adaptive diversity in Levene-type models. *Evol. Ecol. Res.*, **3**: 721–727.

Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *Am. Nat.*, **96**: 361–373.

Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. 1992. How should we define 'fitness' for general ecological scenarios? *TREE*, **7**: 198–202.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. and Van Heerwaarden, J.S. 1996. Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems* (S.J. Van Strien and S.M. Verduyn Lunel, eds.), pp. 183–231. Amsterdam: Elsevier.

Mylius, S.D. and Diekmann, O. 1995. On evolutionary stable life histories, optimisation and the need to be specific about density dependence. *Oikos*, **74**: 218–224.

Neubert, M.G. and Caswell, H. 2000. Density-dependent vital rates and their population dynamic consequences. *J. Math. Biol.*, **41**: 103–121.

Nowak, M. 1990. An evolutionarily stable strategy may be inaccessible. *J. Theor. Biol.*, **142**: 237–241.

Orzack, S.H. and Tuljapurkar, S. 1989. Population dynamics in variable environments. VII. The demography and evolution of iteroparity. *Am. Nat.*, **133**: 901–923.

Parvinen, K. 1999. Evolution of migration in a metapopulation. *Bull. Math. Biol.*, **61**: 531–550.

Ranta, E., Kaitala, V., Alaja, S. and Tesar, D. 2000a. Nonlinear dynamics and the evolution of semelparous and iteroparous reproduction strategies. *Am. Nat.*, **155**: 294–300.

Ranta, E., Tesar, D., Alaja, S. and Kaitala, V. 2000b. Does evolution of iteroparous and semelparous reproduction call for spatially structured systems? *Evolution*, **54**: 145–150.

Ranta, E., Tesar, D. and Kaitala, V. 2002. Environmental variability and semelparity vs. iteroparity as life histories. *J. Theor. Biol.*, **217**: 391–396.

Roff, D. 2002. *Life History Evolution*. Sunderland, MA: Sinauer Associates.

Rueffler, C., Van Dooren, T.J.M. and Metz, J.A.J. 2004. Adaptive walks on changing landscapes: Levins' approach extended. *Theor. Pop. Biol.*, **65**: 165–178.

Schaffer, W.M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology*, **55**: 291–303.

Sibly, R. and Hone, J. 2002. Population growth rate and its determinants: an overview. *Phil. Trans. R. Soc. Lond. B*, **357**: 1153–1170.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

White, A. and Bowers, R.G. 2005. Adaptive dynamics of Lotka-Volterra systems with trade-offs: the role of interspecific parameter dependence in branching. *Math. Biosci.*, **193**: 101–117.