

**Evolutionary Cycling of
Predator-Prey Interactions:
Population Dynamics
and the Red Queen**

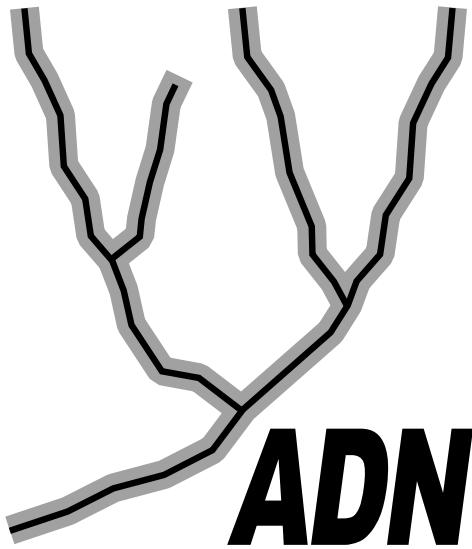
*Ulf Dieckmann, Paul Marrow,
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1996



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Evolutionary Cycling in Predator-Prey Interactions: Population Dynamics and the Red Queen

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This paper describes the coevolution of phenotypes in a community comprising a population of predators and of prey. It is shown that evolutionary cycling is a likely outcome of the process. The dynamical systems on which this description is based are constructed from microscopic stochastic birth and death events, together with a process of random mutation. Births and deaths are caused in part by phenotype-dependent interactions between predator and prey individuals and therefore generate natural selection. Three outcomes of evolution are demonstrated. A community may evolve to a state at which the predator becomes extinct, or to one at which the species coexist with constant phenotypic values, or the species may coexist with cyclic changes in phenotypic values. The last outcome corresponds to a Red Queen dynamic, in which the selection pressures arising from the predator-prey interaction cause the species to evolve without ever reaching an equilibrium phenotypic state. The Red Queen dynamic requires an intermediate harvesting efficiency of the prey by the predator and sufficiently high evolutionary rate constant of the prey, and is robust when the model is made stochastic and phenotypically polymorphic. A cyclic outcome lies outside the contemporary focus on evolutionary equilibria, and argues for an extension to a dynamical framework for describing the asymptotic states of evolution.

1 Introduction

Predator-prey interactions are ubiquitous in nature (Crawley 1992). The ecological interactions between predator and prey species can sometimes be strong enough for the predator to have a major effect on the environment in which the prey is evolving and vice versa. Such interactions have therefore motivated a variety of theoretical models of phenotypic coevolution in predator-prey communities (e.g. Rosenzweig 1973;

Parker 1985; Abrams 1986; Brown and Vincent 1992). Of some interest has been the question as to whether the phenotypes of the predator and prey evolve to an equilibrium asymptotic state such as an evolutionarily stable strategy (Maynard Smith and Price 1973). An alternative could be that their interaction prevents attainment of an equilibrium point and that there is continuous evolutionary change of their phenotypes. Following Van Valen's (1973) Red Queen's hypothesis, the latter behaviour has become known as Red Queen dynamics (Stenseth and Maynard Smith 1984; Rosenzweig et al. 1987; Marrow et al. 1992). To make this notion precise, we refer here to a Red Queen dynamic as any phenotypic dynamic that, in the absence of external forcing, does not tend to an equilibrium state.

In the literature, it has been argued that a Red Queen dynamic would require the set of feasible phenotypes to be unbounded, so that the phenotypes could evolve to ever more extreme states. Rosenzweig et al. (1987) concluded that "the Red Queen depends on the existence of special phenotypic features, i.e. those which are independent, boundless, and about which it may be said, the larger (or smaller, or denser, or furrer, or ...), the better". This requirement is unlikely to be met in reality, and calls into question whether Red Queen dynamics could occur at all. To investigate whether Red Queen dynamics are possible, we have developed models of the evolutionary dynamics of predator and prey phenotypes (Marrow et al. 1992; Marrow and Cannings 1993). These models suggested that, over the course of evolution, the phenotypes could either tend to equilibrium or to non-equilibrium asymptotic states. The models did not incorporate time explicitly, and for this reason could give only qualitative information on the direction of evolution. To determine the asymptotic states of coevolving systems, it is necessary to build the time-dependent processes into the framework of a dynamical system (Dieckmann and Law 1996; Marrow et al. 1996).

In this paper we utilize a hierarchy of three dynamical models to investigate the phenotypic states to which coevolving predators and prey could tend. These models represent different balances between descriptive capacity and corresponding analytic tractability. Mathematical details are given in the Appendix. Section 2 introduces the ecological interactions which define the predator-prey community, and Section 3 briefly explains the distinctive features of the three models used. In Section 4 we demonstrate that the system eventually attains one of three different evolutionary states: (a) the predator goes extinct, (b) coevolution leads to constant phenotypes in predator and prey, and (c) the phenotypes in both species undergo coupled and sustained oscillations on a limit cycle corresponding to Red Queen dynamics. Section 5 analyzes the requirements for this evolutionary cycling. The dependence of cycling on the interaction and mutation structure of the predator and prey is revealed, and we show that the phenomenon is robust under changes in the modelling approach. We conclude that the conceptual framework

of evolutionary theory, with its current focus on fixed points (like evolutionarily stable strategies) as the endpoints of evolution, needs to be expanded to encompass more complex evolutionary attractors such as the limit cycles presented here.

2 The Coevolutionary Community

Our models of phenotypic evolution are underpinned by ecological processes describing the dynamics of predator and prey populations. This ensures that the process of natural selection directing evolution is driven explicitly by the ecology of predator-prey interactions, rather than by an external ad hoc notion of relative fitness of different phenotypes. For simplicity, we focus on a single phenotypic trait in each species; in view of the importance of body size in determining interactions between predator and prey (Cohen et al. 1993), one might think of these traits as body sizes s_1 and s_2 of prey and predator respectively.

To describe the population dynamics in our community, it is necessary to define the ecological processes that affect the population sizes of the two species (Table 1). Table 1a describes the birth and death events that are dependent on phenotype, these being the events that arise from encounters with other individuals, as opposed to the constant birth and death events given in Table 1b.

Evolutionary processes in the community require a mechanism for generating phenotypic variation on which natural selection caused by the interaction between predator and prey can operate. We assume that variation is created by a simple mutation process; in order to keep the analysis tractable we envisage that the genetic systems of the species are clonal. Table 1c shows that each birth event gives rise with probabilities μ_1 and μ_2 to a mutant offspring in the phenotypic traits s_1 and s_2 of prey and predator respectively. The new phenotypes are chosen according to the mutation distributions M_1 and M_2 of prey and predator respectively.

Natural selection arises from the dependence of the birth and death probabilities per unit time α , β , and γ on the phenotypes of the interacting individuals. Various functions could be used for this purpose; we use functions as described in Figure 1. Thus the function α , which characterizes the ecological processes responsible for self-limitation in the prey's population size, is taken to be parabolic such that intermediate phenotypes are favored in the absence of the predator (Figure 1a). The function β describing the effect of a predator on the probability of death of the prey is taken to be bivariate Gaussian (Figure 1b), on the grounds that the predator is likely to show some degree of specialization in the size of prey it chooses relative to its own size (Cohen et al. 1993). On the basis that what is bad for the prey is good for the predator, the function γ

(a) Birth and death processes affected by phenotype			
Target individual	Encountered individual	Birth/death event	Probability of event per encounter per unit time
prey s_1	prey \tilde{s}_1	death of prey s_1	$\alpha(s_1) \dagger$
prey s_1	predator s_2	death of prey s_1	$\beta(s_1, s_2)$
predator s_2	prey s_1	birth predator s_2	$\gamma(s_1, s_2)$
(b) Birth and death processes independent of phenotype			
Target individual		Birth/death event	Probability of event per capita per unit time
prey s_1		birth of prey s_1	r_1
predator s_2		death of predator s_2	r_2
(c) Mutation processes			
Birth event		Mutation event	Probability distribution of event \ddagger
birth of prey s_1		prey $s_1 \rightarrow s'_1$	$(1 - \mu_1) \cdot \delta(s'_1 - s_1) + \mu_1 \cdot M_1(s'_1 - s_1)$
birth of predator s_2		predator $s_2 \rightarrow s'_2$	$(1 - \mu_2) \cdot \delta(s'_2 - s_2) + \mu_2 \cdot M_2(s'_2 - s_2)$

TABLE 1 Definition of birth, death and mutation processes for a prey individual of size s_1 and predator of size s_2 .

\dagger This death event is taken to be dependent only on the phenotype s_1 of the target individual, not on that of the encountered individual \tilde{s}_1 .

\ddagger μ_i is the probability that the birth event in species i is a mutant; δ is the Dirac δ -function; M_i is the mutation distribution.

is related to β by a constant of proportionality, $\gamma = h \cdot \beta$. We call h the harvesting efficiency.

The ecological community presented here extends the model of Marrow et al. (1992) by providing a full dynamical description of the birth, death and mutation processes. It generalizes the former account in the sense that (a) it allows stochastic population dynamics arising from individual-based encounters, and (b) it permits the populations to have polymorphic phenotypic distributions since multiple phenotypic trait values may

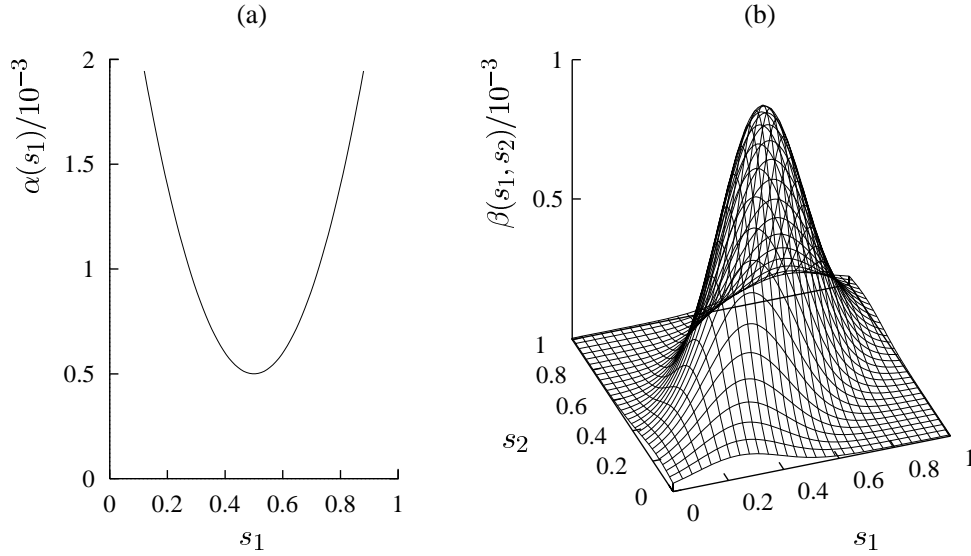


FIGURE 1 Specification of the coevolutionary community given in Table 1. The functions used to describe the effect of phenotype (s_1, s_2) on the birth and death probabilities arising from encounters between individuals are: (a) prey self-limitation $\alpha(s_1)/u = c_1 - c_2s_1 + c_3s_1^2$, (b) effect of predator on prey $\beta(s_1, s_2)/u = \exp(-\delta_1^2 + 2c_4\delta_1\delta_2 - \delta_2^2)$, where $\delta_1 = (s_1 - c_5)/c_6$ and $\delta_2 = (s_2 - c_7)/c_8$, and u is a constant that scales population sizes. Parameters take the values: $c_1 = 3.0$, $c_2 = 10.0$, $c_3 = 10.0$, $c_4 = 0.6$, $c_5 = 0.5$, $c_6 = 0.22$, $c_7 = 0.5$, $c_8 = 0.25$. The function $\gamma(s_1, s_2)$ is not shown since it is related to $\beta(s_1, s_2)$ by the constant of proportionality h . The constant birth and death terms are: $r_1 = 0.5$, $r_2 = 0.05$. Mutation parameters used in the paper are: $\mu_1 = 10^{-3}$, $\mu_2 = 10^{-3}$; M_1 and M_2 are normal distributions with mean 0 and $\sqrt{\text{var}M_1} = 2 \cdot 10^{-3}$, $\sqrt{\text{var}M_2} = 2 \cdot 10^{-3}$, except where otherwise stated. The quantity $u = 10^{-3}$ is constant throughout.

be present simultaneously in each species. From Table 1 we recover as a special case the well-known Lotka-Volterra equations

$$\begin{aligned} \dot{n}_1 &= n_1(+r_1 - \alpha(s_1)n_1 - \beta(s_1, s_2)n_2), \\ \dot{n}_2 &= n_2(-r_2 + \gamma(s_1, s_2)n_1) \end{aligned} \quad (1)$$

for the population sizes n_1 and n_2 of prey and predator respectively, by assuming no mutations, random encounters, deterministic population dynamics (the population sizes of the species are large), and monomorphic phenotypic distributions (only one phenotype present within each species).

3 Three Dynamical Models of Coevolution

Equations 1 illustrate how the general coevolutionary process defined in Table 1 can be reduced by making appropriate simplifying assumptions. In a similar spirit, three dynamical models are derived in the Appendix for the change in phenotypic traits s_1 and s_2 of the prey and predator respectively.

1. *Polymorphic stochastic model.* This provides a full description of the dynamics defined in Table 1. It can be given as a multivariate functional master equation, and depends only on the assumption of random encounters, thus allowing both for polymorphism and for stochasticity.
2. *Monomorphic stochastic model.* This retains the stochasticity arising from mutation in the coevolutionary process, but assumes that variation in the phenotypic distributions is small enough for an assumption of monomorphism to provide a good approximation. The coevolutionary process can then be described as a directed random walk in the phenotype space spanned by s_1 and s_2 . Stochastic steps occur when a resident phenotype is replaced by an advantageous mutant, e.g. $s_1 \rightarrow s'_1$; a sequence of such substitutions is called a trait substitution sequence (Metz et al. 1992). The model is framed as a multivariate master equation.
3. *Monomorphic deterministic model.* This is a deterministic approximation to the monomorphic stochastic model above. It is given in terms of a system of ordinary differential equations describing the expected evolutionary paths in the phenotype space.

Further information as to the relation between the three models is given in the Appendix and in Dieckmann (1994). The full derivation of the monomorphic models is given in Dieckmann and Law (1996), and a discussion of the third model can be found in Marrow et al. (1996).

4 Evolutionary Outcomes

Here we describe the variety of possible evolutionary outcomes in a predator-prey community, using the monomorphic deterministic model. Deterministic dynamics of this kind have been used elsewhere in the literature (e.g. Hofbauer and Sigmund 1990; Vincent 1991; Abrams et al. 1993), but have not previously been underpinned by a formal derivation.

In the case of the monomorphic dynamics we can immediately infer from equations (1) that there is a region in the phenotype space where both species can coexist with positive population densities. The boundary of this region is depicted by the oval discontinuous curves in Figure 2. Only within this region can the predator population harvest the prey sufficiently to survive; given a pair of phenotypes (s_1, s_2) outside this

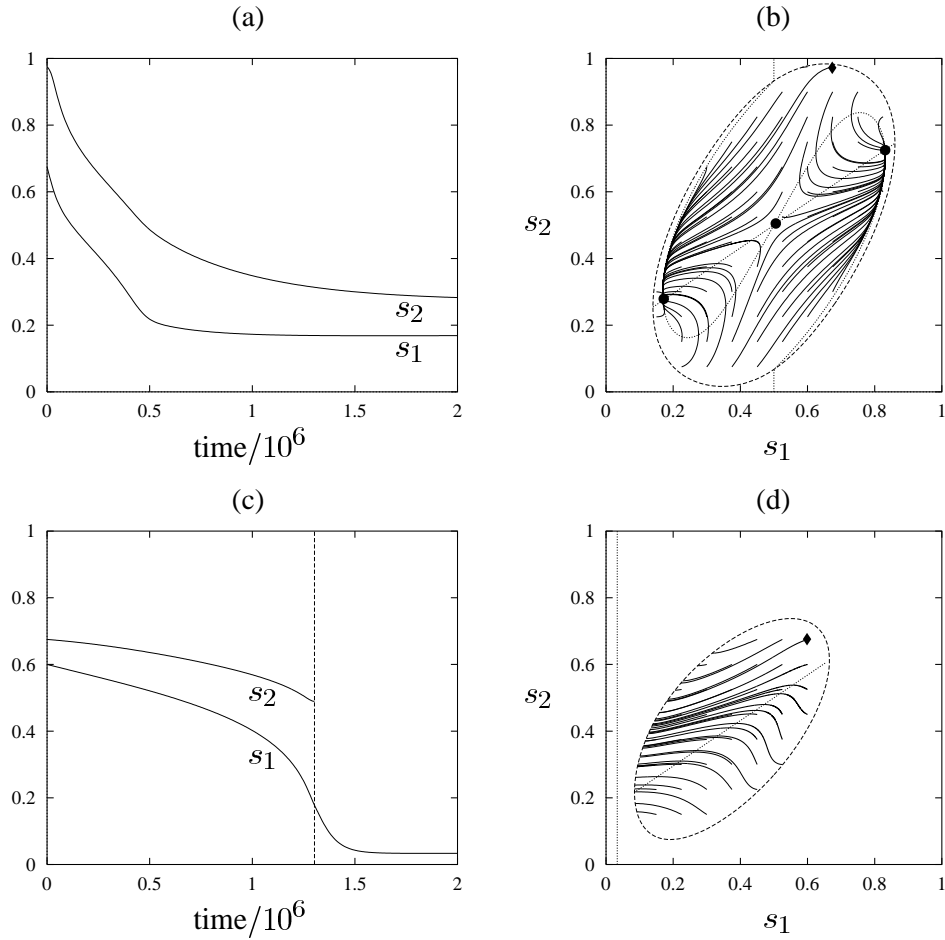


FIGURE 2 Patterns of evolution of prey (s_1) and predator (s_2) phenotypes obtained from the monomorphic deterministic model. (a) Solution that tends to an equilibrium point over the course of time obtained using the parameter values in Figure 1 with $h = 1$. (b) Phase portrait of the phenotype space from which (a) is drawn with orbits shown as continuous lines; the starting point of the orbit corresponding to the solution in (a) is shown as the diamond. The boundary of the region of coexistence of the predator and prey is given as the discontinuous oval line. Isoclines are shown as dotted lines (straight line: predator; curved line: prey); equilibrium points occur at the intersection of the isoclines and are indicated by the filled circles. (c) Solution for a community that evolves to predator extinction at time $= 1.30 \cdot 10^6$. After this time, the prey continues to evolve in the absence of the predator. Parameter values as in Figure 1, except $c_1 = 1.0$, $c_2 = 1.0$, $c_3 = 15.0$, and with $h = 1$. (d) Phase portrait of the phenotype space from which solution (c) is drawn; the starting point of the orbit corresponding to the solution in (c) is shown as the diamond. The prey isocline lies outside the region of coexistence and orbits touch the boundary of the region of coexistence at which point the predator goes extinct.

region, the predator population is driven to extinction by the population dynamics (1). Accordingly, coevolution of the predator and prey can only be observed within this region of coexistence.

For a coevolving predator-prey community starting with phenotypes in the region of coexistence, there are eventually three possible outcomes.

1. *Evolution to a fixed point.* In Figure 2a, the phenotypic values tend to an equilibrium point; once this is reached, no further evolution occurs. There are in fact three fixed points at the intersection of the isoclines (i.e. at $\dot{s}_1 = 0$, $\dot{s}_2 = 0$, see Appendix) in this example, as can be seen from the accompanying phase portrait (Figure 2b); two of these are attractors and they are separated by the stable manifold of the third which is a saddle point. Notice that the coevolutionary process here is multistable with two attractors having disjunct domains of attraction; thus there may be no more reason for a particular observed asymptotic state than the more or less arbitrary initial conditions.
2. *Evolution to extinction.* In Figure 2c the coevolutionary process drives the phenotypic values towards the boundary of the region of coexistence (see Figure 2d). There the predator population goes extinct and the predator phenotype is no longer defined. The phenotype space of the community collapses from (s_1, s_2) to the one dimensional space s_1 , where the prey phenotype continues to evolve to its own equilibrium point. Note here that the extinction of the predator is driven by the evolutionary dynamics in (s_1, s_2) and not merely by the population dynamics in (n_1, n_2) .
3. *Evolutionary cycling.* In Figure 3a, the coevolutionary process in the predator-prey community continues indefinitely; mutants replace residents in a cyclic manner such that the phenotypes eventually return to their original values and do not reach an equilibrium point. As can be seen from Figure 3b, the attractor is a limit cycle, confirming the conjecture made by Marrow et al. (1992) that Red Queen coevolution can occur in this predator-prey community.

These three outcomes of coevolution correspond to the endpoints of evolutionary arms races discussed qualitatively by Dawkins and Krebs (1979), namely: (i) equilibrium endpoints, (ii) one side wins, and (iii) cyclic endings.

5 Requirements for Cycling

Here, we investigate the robustness of the phenomenon of evolutionary cycling. We do this in two ways. First a bifurcation analysis of the monomorphic deterministic model is given; this allows one to establish the range of parameters in the model that permit evolutionary cycling to occur. Second, we examine the monomorphic stochastic model and finally the polymorphic stochastic model to see how robust the phenomenon of evolutionary cycling is when the simplifying assumptions of the monomorphic deterministic model are removed.

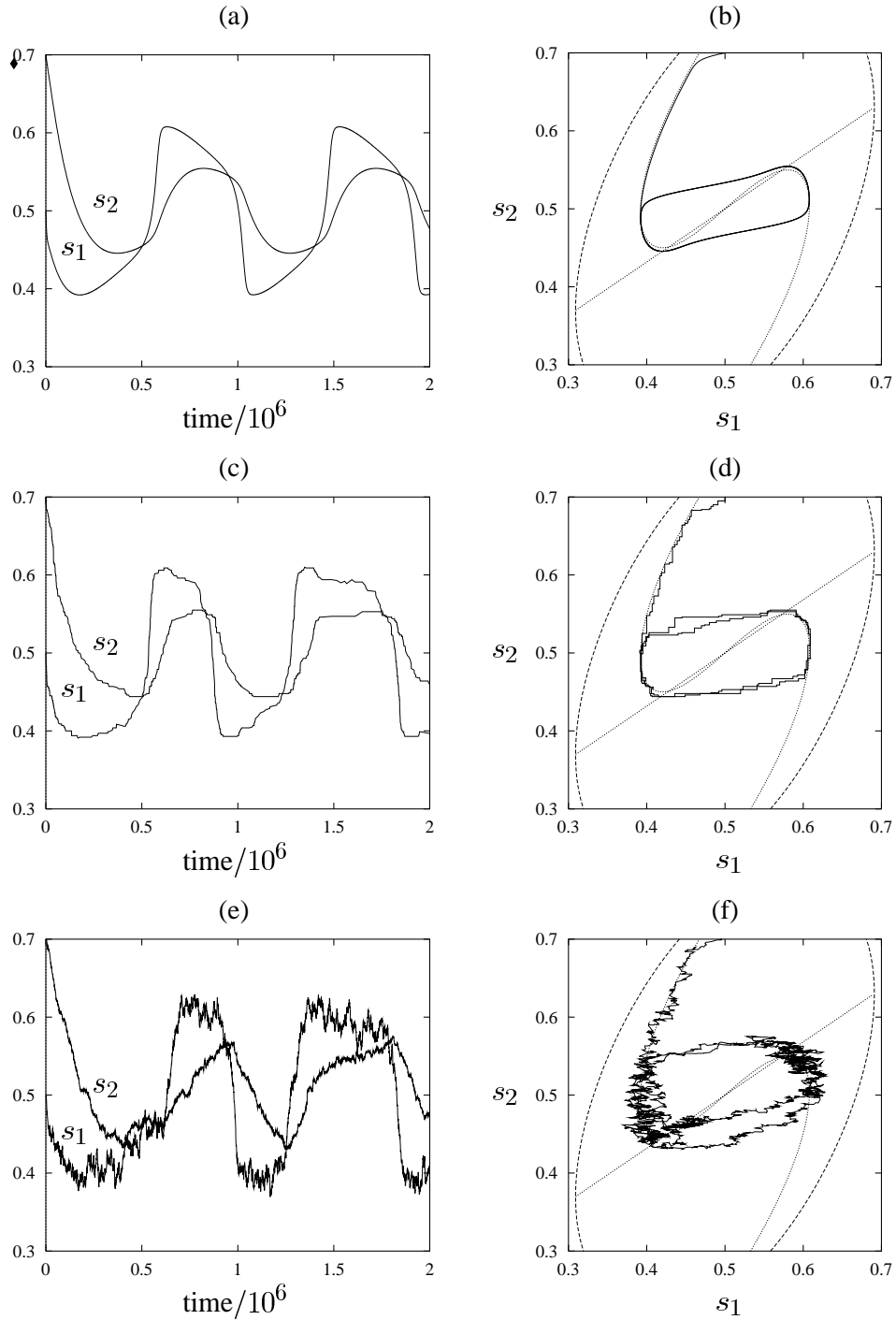


FIGURE 3 Example of evolutionary cycling using the monomorphic deterministic model in (a) and (b), the monomorphic stochastic model in (c) and (d), and the polymorphic stochastic model in (e) and (f). Graphs (a), (c) and (e) show the values of the prey (s_1) and predator (s_2) phenotypes as functions of time (mean values in the case of the polymorphic model). The corresponding orbits are shown as continuous lines in the phase spaces given in graphs (b), (d) and (f). See Figure 2 for an explanation of the phase portrait. Parameter values for these simulations are identical and are set as given in Figure 1, except $\mu_1 = 10^{-2}$, $\mu_2 = 10^{-2}$ and with $h = 0.14$.

5.1 BIFURCATION ANALYSIS OF THE MONOMORPHIC DETERMINISTIC MODEL

We focus attention on the effect of two quantities of particular interest from an ecological viewpoint. These are firstly the predator's efficiency in harvesting the prey as given by the ratio $h = \gamma/\beta$, and secondly the ratio of the evolutionary rate constants $r = (\mu_1 \text{var}M_1)/(\mu_2 \text{var}M_2)$ (see Appendix). The results of the bifurcation analysis are presented in Figure 4a. Four distinct regions within the parameter space can be seen:

1. For $h < 5\%$ the two species cannot coexist, and therefore no coevolution can occur.
2. For $5\% < h < 9.8\%$ there exists only one fixed point for the monomorphic deterministic model. This fixed point is an attractor; the system evolves to this point and there is no further coevolution once it is reached.
3. For $h > 14.8\%$ there exist three fixed points of the dynamics. The two outer points are stable, and which of these is reached depends on the phenotypes initially present.
4. For $9.8\% < h < 14.8\%$ and sufficiently high values of r (Figure 4a), the attractor turns into a limit cycle, giving rise to Red Queen dynamics. On the other hand, for low values of r , the limit cycle breaks down and we recover the dynamical behavior of cases 2 and 3 with the switch occurring at $h = 12.6\%$.

The boundary of region 4 is in fact slightly more complicated than the description above suggests because two further kinds of dynamics can occur here: (i) a limit-cycle attractor around each of the outer fixed points, and (ii) a limit-cycle attractor around all three fixed points with each of the outer fixed points also being an attractor. But the parameter space permitting these dynamics is very small compared to the others and they are therefore of less biological interest. We conclude that evolutionary cycling requires an intermediate harvesting efficiency plus prey evolution to occur sufficiently fast compared to predator evolution.

The results from the bifurcation analysis are intuitive in that evolutionary cycling requires: (i) the effect of selection by the predator on the prey to be great enough to drive the prey from the phenotypic equilibrium it would have in the absence of the predator (h not too low), (ii) sufficient need for the predator to track the prey's phenotypic change (h not too high), and (iii) in the resulting evolutionary race the prey must be fast enough not to be 'caught up' by the predator (r not too low). In view of the respiratory costs that the predators have to meet from consumption of prey simply to stay alive, one would expect h to be substantially less than 1 and evolutionary cycling to occur in a range of h likely to be observed in reality.

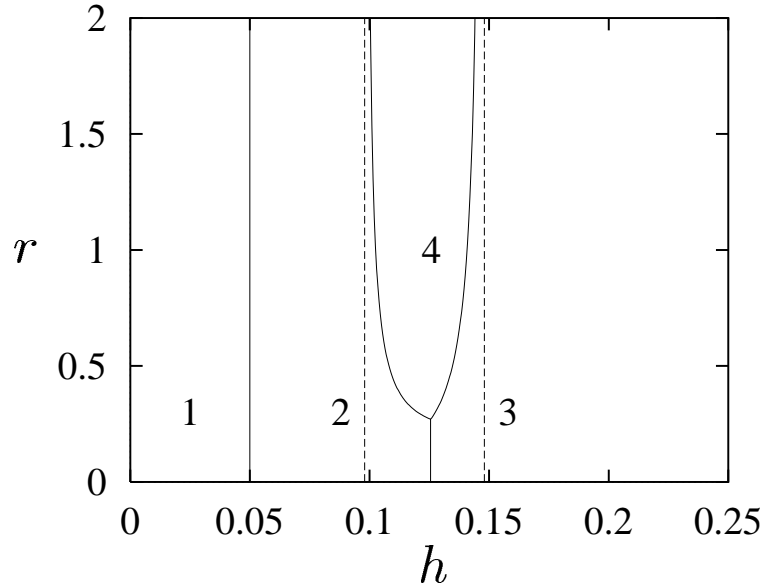


FIGURE 4 Results of bifurcation analysis, showing the effect of the harvesting efficiency h , and the ratio of the evolutionary rate constants r on the dynamics of the monomorphic deterministic model. Regions are: (1) predator absent, (2) one fixed point present, which is an attractor, (3) three fixed points, two of which are attractors, (4) limit cycle attractor.

5.2 MONOMORPHIC STOCHASTIC MODEL

A realization of the monomorphic stochastic dynamics is given in Figures 3c and 3d. The parameter values used are the same as those in Figures 3a and 3b, and we see that the cyclic behaviour is still maintained. In addition two major new effects should be noted. First, it can be seen that the oscillations in phenotypic values do not all have the same period. This phenomenon, which is well known in the theory of stochastic processes (phase diffusion, Tomita et al. 1974), comes about because stochastic perturbations along the limit cycle are not balanced by a counteracting force, whereas those orthogonal to the limit cycle are. Second, limit cycles whose extension in phenotype space is small relative to the typical mutational step sizes (given by $\sqrt{\text{var}M_1}$ and $\sqrt{\text{var}M_2}$) will be obscured by the stochastic noise. The boundaries of region 4 (Figure 4a) will then be less sharp than those in the monomorphic deterministic model, as illustrated in Figure 4b. Thus, if the evolutionary cycling is to be visible, the mutational steps must not be too large.

5.3 POLYMORPHIC STOCHASTIC MODEL

A realization of the polymorphic stochastic model is shown in Figures 3e and 3f, using as before the parameter values of Figures 3a and 3b. The phenomenon of evolutionary cycling still persists despite the phenotypic distributions now being polymorphic. In addition, this model allows for the effects of demographic stochasticity also of the resident phenotypes (see Appendix). Although this superimposes more random variation to the solution, cycling is maintained. Provided that phenotypic variance is not too large and population sizes are not too small, we thus can conclude that evolutionary cycling is robust to relaxation of the simplifying assumptions of the monomorphic deterministic model, and that it can actually occur in predator-prey communities like the one defined in Section 2.

6 Discussion

The main result of this analysis is that evolutionary limit cycles, in which the predator and prey phenotypes continue to change indefinitely, are a natural outcome in a coevolutionary community. The cyclic behaviour is not an artefact of determinism or monomorphism, because the phenomenon can be observed both in the stochastic monomorphic simulations and in the stochastic polymorphic ones. Clearly there is no general rule in nature to say that phenotypic evolution would lead to an equilibrium point in the absence of external changes in the environment.

A simple classification of the outcomes of phenotypic evolution can be constructed from two dichotomies. The first depends on whether an attractor exists, and the second on whether the attractor is a fixed point. This gives three classes of dynamics:

- (i) evolution to a fixed-point attractor with stationary phenotypes,
- (ii) evolution to an attractor that is not a fixed point on which the phenotypes continue to change indefinitely, and
- (iii) evolution without an attractor, such that the phenotypes take more and more extreme values.

According to the definition in the Introduction, Red Queen dynamics would encompass both class (ii) and class (iii). Class (iii) is unrealistic for most kinds of phenotypes and, if the Red Queen were to depend on the existence of such dynamics in nature, one could reasonably conclude that Red Queen dynamics would be very unusual (Rosenzweig et al. 1987). But this would be to miss class (ii), and dynamics of this kind we have shown here to be feasible. In fact the limit cycle is but one of a number of non-equilibrium attractors; for instance in systems with more than two coevolving species, chaotic evolutionary attractors could be found.

Cyclic phenotype dynamics can occur in coevolution as is well known from theoretical studies of genetic polymorphisms under frequency-dependent selection (e.g. Akin 1981; Seger 1992), and research into the dynamics of strategy frequencies (Nowak and Sigmund 1989). The system considered here is different in two respects. First, the trait values are continuous, whereas cyclic dynamics have typically been observed in polymorphic systems with large qualitative differences between a small number of coexisting phenotypes. Second, and more important, the underlying genetic process here would be a sequence of gene substitutions in which mutants keep replacing the resident types rather than one in which the genes always coexist and undergo oscillations in frequency. Thus we are here looking at a process operating on an altogether larger evolutionary scale, such that the populations can undergo drastic changes in their phenotypic state, and still return to some earlier value.

The monomorphic deterministic dynamic described here in fact turns out to be canonical (Dieckmann and Law 1996), and can be derived from other starting points such as quantitative genetics (Abrams et al. 1993). It seems therefore that there is a large class of models of phenotypic coevolution with the potential for non-equilibrium asymptotic states. This needs to be emphasized because the assumption that asymptotic states of evolution are fixed points underlies much contemporary evolutionary thought. This assumption and the techniques that go with it (in particular evolutionarily stable strategies) are clearly not appropriate for dealing with non-equilibrium asymptotic states. The prevailing view among evolutionary biologists, centred on equilibrium points, needs to be extended to a dynamical framework to assimilate the Red Queen.

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Appendix

In this appendix we provide a brief derivation of the three dynamical models describing the process of coevolution for the reader interested in the more technical details. The theory outlined here is general in so far as it applies to a large variety of N -species coevolutionary communities of which the predator-prey system analyzed in this paper is just a particular instance.

THE POLYMORPHIC STOCHASTIC MODEL

At time t there are n_i individuals in species i with $i = 1, \dots, N$. These have phenotypes s_{ij} with $j = 1, \dots, n_i$ such that the phenotypic distribution $p_i(s_i)$ in species i is given by

$$p_i = \sum_{j=1}^{n_i} \delta_{s_{ij}} \quad (\text{A.1})$$

with $\delta_x(y) = \delta(x - y)$ where δ denotes Dirac's δ -function. These distributions change in time due to stochastic birth, death and mutation processes like those specified in Table 1.

The dynamics of the phenotypic distributions can be described by a functional master equation for $P(p, t)$, the probability density of $p = (p_1, \dots, p_N)$ to be realized at time t (Dieckmann 1994). The algorithm derived from this equation is the following.

1. Initialize the phenotypic distributions p_i with $i = 1, \dots, N$ at time $t = 0$ and specify the time T when to stop the dynamics.
2. Calculate the birth and death probabilities $b_i(s_{ij}, p)$ and $d_i(s_{ij}, p)$ for each individual $i = 1, \dots, N$, $j = 1, \dots, n_i$ with phenotype s_{ij} in the environment given by p .

Remark. According to Table 1 we have for the predator-prey community $b_1(s_1, p) = r_1$, $d_1(s_1, p) = \int \alpha(s_1) p_1(\tilde{s}_1) d\tilde{s}_1 + \int \beta(s_1, s_2) p_2(s_2) ds_2$, $b_2(s_2, p) = \int \gamma(s_1, s_2) p_1(s_1) ds_1$, and $d_2(s_2, p) = r_2$.

3. Construct the sums $w_{ij} = b_i(s_{ij}, p) + d_i(s_{ij}, p)$, $w_i = \sum_{j=1}^{n_i} w_{ij}$ and $w = \sum_{i=1}^N w_i$ with $i = 1, \dots, N$, $j = 1, \dots, n_i$.
4. Choose the waiting time Δt for the next event to occur according to $\Delta t = -\frac{1}{w} \ln r$ where $0 < r \leq 1$ is a uniformly distributed random number.
5. Choose species i with probability $\frac{1}{w} w_i$. Choose individual j in species i with probability $\frac{1}{w_i} w_{ij}$. Choose then a birth or death event with probability $\frac{1}{w_{ij}} b_i(s_{ij}, p)$ and $\frac{1}{w_{ij}} d_i(s_{ij}, p)$ respectively.
6. If a birth event occurs for an individual with phenotype s_{ij} , choose a new phenotype s'_{ij} with probability density $(1 - \mu_i) \delta(s'_{ij} - s_{ij}) + \mu_i M_i(s'_{ij} - s_{ij})$.
7. Update time and phenotypic distributions according to $t \rightarrow t + \Delta t$ and $p_i \rightarrow p_i + \delta_{s'_{ij}}$ or $p_i \rightarrow p_i - \delta_{s_{ij}}$ for a birth or death event in species i respectively.
8. Continue from Step 2 until $t \geq T$.

The protocol above utilizes the minimal process method (Gillespie 1976) to simulate the functional master equation. Note in particular that according to Step 4 the waiting times follow an exponential distribution, the standard result for stochastic processes described by homogeneous master equations.

THE MONOMORPHIC STOCHASTIC MODEL

If μ_i is sufficiently small for all $i = 1, \dots, N$ the phenotypic distributions in each species will be sharply concentrated around a single phenotype, the resident phenotype. The distributions then are called monomorphic (precisely one should refer to them as quasi-monomorphic since still more than one phenotype may be present in the population) and can well be approximated by $p_i = n_i \delta_{s_i}$ with resident phenotype s_i and population size n_i . In this case phenotypic change occurs via a sequence of trait substitutions where a resident phenotype s_i is replaced by a mutant phenotype s'_i (Dieckmann 1994).

The resulting directed random walk in the phenotype space is described by the master equation

$$\frac{d}{dt} P(s, t) = \int \left[w(s|s') P(s', t) - w(s'|s) P(s, t) \right] ds' \quad (\text{A.2})$$

where $P(s, t)$ denotes the probability density of the resident phenotypes to be given by $s = (s_1, \dots, s_N)$ at time t . Equation (A.2) only holds if the stochastic dynamics of s are a Markov process; to guarantee this it can be necessary to consider more than one trait per species. This more general case is analyzed in Dieckmann and Law (1996). In the infinitesimal time interval dt a trait substitution in only a single trait can occur and

thus the probability per unit time $w(s'|s)$ for the transition $s \rightarrow s'$ can be decomposed according to

$$w(s'|s) = \sum_{i=1}^n w_i(s'_i, s) \prod_{\substack{j=1 \\ j \neq i}}^n \delta(s'_j - s_j). \quad (\text{A.3})$$

Here $w_i(s'_i, s)$ denotes the probability per unit time for a trait substitution $s_i \rightarrow s'_i$ to occur in species i given an environment of phenotypes s .

A trait substitution requires that, first, a specific mutant phenotype s'_i enters the population of species i and, second, that it succeeds in replacing the resident phenotype s_i . Since these two processes are statistically independent, their probabilities multiply and $w_i(s'_i, s)$ is given by the product

$$w_i(s'_i, s) = \underbrace{\mu_i b_i(s_i, s) n_i(s)}_{\text{term I}} \underbrace{M_i(s'_i - s_i)}_{\text{b}} \underbrace{b_i^{-1}(s'_i, s) (f_i(s'_i, s))_+}_{\text{term II}}. \quad (\text{A.4})$$

The functions $b_i(s'_i, s)$, $d_i(s'_i, s)$ and $f_i(s'_i, s) = b_i(s'_i, s) - d_i(s'_i, s)$ denote the per capita birth, death and growth probabilities per unit time (or rates) of a phenotype s'_i in an environment given by the phenotypes s . They are defined in terms of the analogous quantities of the polymorphic stochastic model by e.g. $b_i(s'_i, s) = b_i(s'_i, p)$ with $p = (n_1(s)\delta_{s_1}, \dots, n_N(s)\delta_{s_N})$. Here the population sizes $n_i(s)$ are determined as the equilibrium solutions of the resident's population dynamics $\frac{d}{dt}n_i = n_i f_i(s_i, s)$. The general case of nonequilibrium population dynamics is treated in Dieckmann and Law (1996). A more formal analysis is given in Rand et al. (1993)

Remark. For the predator-prey community we obtain $b_1(s'_1, s) = r_1$, $d_1(s'_1, s) = \alpha(s'_1)n_1(s) + \beta(s'_1, s_2)n_2(s)$, $b_2(s'_2, s) = \gamma(s_1, s'_2)n_1(s)$, and $d_2(s'_2, s) = r_2$.

We now explain the different terms in equation (A.4).

1. Term I represents the impact of the mutation process and is given by weighting (a) the probability per unit time for any mutant to occur in the resident population of phenotype s_i by (b) the probability density for the mutant phenotype to be given by s'_i . Since mutations in distinct individuals are statistically uncorrelated, term Ia is composed of three factors. The per capita birth rate $b_i(s_i, s)$ of the resident phenotype is multiplied by μ_i , the mutation probability for each birth event, giving the per capita mutation rate of the resident phenotype. This is multiplied by the resident's population size n_i to yield the mutation rate of the resident population. Term Ib simply is the mutation distribution $M_i(s'_i - s_i)$ for mutant phenotypes s'_i given the resident phenotype s_i .

2. Term II stands for the process of selection. In the monomorphic stochastic model it is assumed that the resident populations are sufficiently large not to be subject to accidental extinction due to stochastic fluctuations of their population sizes. In contrast, the mutant population starts with population size 1 such that the impact of demographic stochasticity on its dynamics ought to be considered. Since the function $(\cdot)_+$ returns its argument if the argument is positive and 0 otherwise, deleterious mutants, with $f_i(s'_i, s) < 0$, have no chance to survive in the resident population. But even advantageous mutants, with $f_i(s'_i, s) > 0$, experience some risk of accidental extinction due to random sampling when initially rare (Fisher 1958). Term II also shows that for large initial per capita growth rates of the mutant the probability for it to succeed in replacing the resident saturates at 1. The exact form of term II is derived in Dieckmann and Law (1996).

Combining equations (A.2), (A.3) and (A.4) yields a complete description of the stochastic coevolutionary dynamics provided that phenotypic distributions are sufficiently concentrated and that population sizes are sufficiently large. The algorithm for this model again follows the minimal process method.

THE MONOMORPHIC DETERMINISTIC MODEL

To capture the representative features of the monomorphic coevolutionary dynamics directly, rather than having to consider a large number of different realizations of the monomorphic stochastic model, a deterministic approximation of the latter is devised. The deterministic path $\langle s \rangle$ associated with a stochastic process is described by the equation (Serra et al. 1986)

$$\frac{d}{dt}\langle s \rangle = a(\langle s \rangle) \quad (\text{A.5})$$

where the function a is the first jump moment of the stochastic process whose components in our case are given by

$$a_i(s) = \int (s'_i - s_i) w_i(s'_i, s) ds'_i \quad (\text{A.6})$$

with $i = 1, \dots, N$. If the different realizations of the stochastic process do not spread too far apart, i.e. if the variance of the probability density $P(s, t)$ in equation (A.2) stays small, the deterministic path $\langle s \rangle$ provides a good approximation of the mean path $\int s P(s, t) ds$ (van Kampen 1981).

We obtain the deterministic monomorphic model by introducing equation (A.4) into (A.6). To simplify the result, we expand the functions $f_i(s'_i, s)$ and $b_i^{-1}(s'_i, s)$ in the mutant phenotype s'_i about the resident phenotype s_i . Here we only present the first order result for symmetric mutation distributions, the derivation of higher order correction

terms and for arbitrary mutation distributions is given in Dieckmann and Law (1996). By introducing the result into equation (A.5) we obtain the deterministic path of the monomorphic stochastic model

$$\frac{d}{dt}\langle s_i \rangle = \underbrace{\left(\frac{1}{2} \mu_i \text{var} M_i \right) n_i(\langle s \rangle)}_{\text{term I}} \underbrace{\frac{\partial}{\partial s'_i} f_i(s'_i, \langle s \rangle) \Big|_{s'_i = \langle s_i \rangle}}_{\text{term II}} \quad (\text{A.7})$$

for $i = 1, \dots, N$. The deterministic path thus is described by a simple, though typically nonlinear, dynamical system composed of N coupled first order differential equations. The terms on the right hand side of equation (A.7) have the following meanings.

1. Term I again captures the influence of mutation on the coevolutionary dynamics. The factor $\frac{1}{2} \mu_i \text{var} M_i$, called the evolutionary rate constant, is affected by the proportion μ_i of births that produce mutants and by the variance $\text{var} M_i$ of the mutation distribution in the trait s_i . Together with the population size n_i all these terms are non-negative, so term I as a whole serves to scale the rate of evolutionary change.
2. Term II accounts for the impact of selection as it determines the direction of evolutionary change. When this derivative of the per capita growth rate f_i is positive (respectively negative), mutants with increased (respectively decreased) phenotypic values s_i will be advantageous in the environment given by $\langle s \rangle$. The lines on which the terms II are zero are the isoclines of the monomorphic deterministic dynamics.

The Runge-Kutta method can be employed to construct an algorithm for the monomorphic deterministic model. Equations (A.7) have features in common with other models of adaptive dynamics (Hofbauer and Sigmund 1990; Vincent 1991; Abrams et al. 1993) but are here explicitly derived from the underlying stochastic ecological processes.