

On evolution under asymmetric competition

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Summary

The evolutionary consequences of asymmetric competition between species are poorly understood in comparison with symmetric competition. A model for evolution of body size under asymmetric competition within and between species is described. The model links processes operating at the scale of the individual to that of macroscopic evolution through a stochastic mutation–selection process. Phase portraits of evolution in a phenotype space characteristically show character convergence and parallel character shifts, with character divergence being relatively uncommon. The asymptotic states of evolution depend very much on the properties of asymmetric competition. Given relatively weak asymmetries between species, a single equilibrium point exists; this is a local attractor, and its position is determined by the intra- and interspecific asymmetries. When the asymmetries are made stronger, several fixed points may come about, creating further equilibrium points which are local attractors. It is also possible for periodic attractors to occur; such attractors comprise Red Queen dynamics with phenotype values that continue to change without ever settling down to constant values. From certain initial conditions, evolution leading to extinction of one of the species is also a likely outcome.

Keywords: adaptive dynamics; asymmetric competition; co-evolution; competition; evolutionarily stable strategy; frequency-dependent selection; Red Queen dynamics; Stochastic process

Introduction

Asymmetric competition arises when, during an encounter between two or more individuals for some limited resource, these resources are divided up unequally: the larger individual wins the contest (Clutton-Brock *et al.*, 1979), the territory holder keeps the territory (Davies, 1978), the taller plant gets more light (Weiner, 1990). Such asymmetries are known to be a common phenomenon in nature (Lawton and Hassell, 1981; Connell, 1983; Schoener, 1983; Weiner, 1990), and are therefore likely to be an important force of natural selection. Asymmetric competition has a special interest because it does not necessarily cause evolution of weak interactions among species, as one might expect through divergent character displacement (the ‘ghost of competition past’: Connell, 1980). Thus natural selection generated by asymmetric competition is likely to be a persistent and continuing phenomenon in communities.

In view of the importance of asymmetric competition between species, it is surprising how little understanding there is of its evolutionary effects, both empirically and theoretically. Interest has focused more on interactions *within* species and how these contribute to arms races and cyclic changes in phenotype (Maynard Smith, 1982, p. 94 *et seq.*; Parker, 1983; Maynard Smith and Brown, 1986; Abrams and Matsuda, 1994; Matsuda and Abrams, 1994). There has, however, been some study of the role of asymmetries in the taxon cycles of *Anolis* lizards (Rummell and Roughgarden, 1983, 1985; Taper and Case, 1992a), and some more general discussion of the

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evolutionary consequences of asymmetric competition (Abrams, 1987; Abrams *et al.*, 1993a; Abrams and Matsuda, 1994).

Studies of asymmetric competition in the empirical literature are of three main kinds, distinguished by the temporal scale at which the process is studied. Those at the smallest, *microscopic* scale deal with encounters between individuals which depend on behavioural mechanisms of competition between animals (Perfecto, 1994; Robinson and Terborgh, 1995), and on short-term effects of neighbours on growth in plants (Goldberg, 1987). Those at the intermediate, *mesoscopic* scale are concerned with population dynamics, often involving the manipulation of densities of pairs of species in a reciprocal manner. Asymmetries are commonly found in these studies, one species being much more affected by the manipulations than the other (Lawton and Hassell, 1981; Morin and Johnson, 1988; Thompson and Fox, 1993). Studies at the largest temporal scale, the *macroscopic* scale of phenotype evolution, attempt to account for phenotype patterns across species as an outcome of evolution driven by asymmetric competition. Such patterns include the differences in body size of lizard species when they co-exist on islands, in contrast to their intermediate sizes on islands where only one species occurs (Case and Bolger, 1991). The *Anolis* lizards of the Lesser Antilles have been studied in greatest detail, and there is fossil evidence suggesting that co-existing *Anolis* species gradually decline in body size. The larger *Anolis* species are thought to do so at a faster rate, leading to extinction of the smaller species, the taxon cycle eventually repeating itself by invasion of a new species of large body size from the mainland (Roughgarden and Pacala, 1989).

In this paper, we link together these three time-scales in a formal model of phenotypic evolution of two interacting species. The idea is to apply a single theoretical framework across the time-scales to retain explicitly the individual-based ecological processes ultimately responsible for natural selection (Marrow *et al.*, 1992; Dieckmann, 1994; Dieckmann and Law, 1996; Marrow *et al.*, 1996). This entails deriving a model of macroscopic phenotype dynamics as an approximation to a stochastic mutation–selection process (Dieckmann and Law, 1996), where individuals with different phenotypic values arise by mutation and replace one another in a trait substitution sequence (Metz *et al.*, 1992). Our intention is to complement earlier research, which was based on quantitative genetics, by making explicit the randomness associated with mutation and survival of mutants when rare. Our approach also differs from previous theory on taxon cycles (Rummell and Roughgarden, 1983, 1985; Brown and Vincent, 1987; Taper and Case, 1992a), in that asymmetric competition becomes monotonically greater the larger the phenotypic difference between individuals. This earlier work, motivated by resource utilization functions, assumed that, if the phenotypic difference was large enough, there would be no interaction. We want to add to this, because some kinds of interspecific competition are intrinsically asymmetric however great the phenotypic difference. Such asymmetries include, for instance, that between tall and short plants in competition for light, and the asymmetry between large and small individuals in aggressive interactions.

We give our results in the form of phase portraits of the evolutionary dynamics in a two-dimensional phenotype space. These portraits show that modifications to the properties of asymmetric competition can cause a diverse range of evolutionary outcomes, with multiple local attractors leading to the extinction of one species or the co-existence of both species. [Multiple local attractors should not be confused with single equilibrium points that allow multiple strategies within species at an ESS (Vincent and Brown, 1988).] In cases where the species co-exist, the attractors may be fixed points or cyclic orbits. The fixed points have the property that only one of the species is uninvadable to mutants (i.e. at an ESS); the other is at a fitness minimum. The cyclic orbits can be thought of as ‘Red Queen’ dynamics, from Van Valen’s (1973) Red Queen’s hypothesis, as phenotype dynamics that do not tend to a fixed point in the absence of external forcing (Dieckmann *et al.*, 1995).

Theory

In the theory developed below, we assume that the evolving community comprises two species. Individuals are distinguished by the value of some phenotypic trait, denoted s_i for an individual of species i (where $i = 1, 2$). The phenotype values are continuous and drawn from the sets s_i , scaled so that $s_i \in (0, 1)$. It is convenient, but by no means essential, to think of the traits as body size in view of the well-documented effect this has on asymmetric competition (Clutton Brock *et al.*, 1979; Weiner, 1990). The intention is to describe how these traits evolve under natural selection due to asymmetric competition between and within species. We investigate this by constructing a model for macroscopic phenotypic evolution from microscopic encounters between individuals and mesoscopic population dynamics.

The ecological assumptions made below are needed simply to specify a model system, and can readily be altered to match the behaviour of particular ecological interactions. On the other hand, the evolutionary assumptions, labelled (A1) to (A3), are structural and needed in the derivation of the macroscopic evolutionary dynamic.

Encounters between individuals (microscopic scale)

Asymmetric competition has the property that, when two individuals encounter one another as they search for resources, the effect on them is unequal. We assume that eventually this is transformed into different probabilities of death, α_{ij} (per encounter per unit time), for the two individuals, and describe the asymmetry as:

$$\alpha_{ij}(s_i, s_j)/\gamma = c_{ij} \left(1 - \frac{1}{1 + u_{ij}(s_i, s_j)} \right) \quad \text{for } i, j = 1, 2 \tag{1}$$

where $u_{ij}(s_i, s_j) = \exp(-k_{ij} \cdot (s_i - s_j))$.

The first argument, s_i , is the body size of the individual whose mortality risk we wish to determine, and the second, s_j , is the body size of the other individual. Parameters c_{ij} and k_{ij} are positive and non-negative respectively. The parameter γ has dimensions time^{-1} and scales the population sizes. Body size can be thought of as log-transformed when the asymmetry depends on body-size ratios rather than differences (Schwinning and Fox, 1995). The scaling $s_i \in (0, 1)$ can be achieved by the transformation:

$$s_i = \log \left(\frac{I_i}{I_{i,\min}} \right) / \log \left(\frac{I_{i,\max}}{I_{i,\min}} \right) \tag{2}$$

where the untransformed trait value is $I_i \in (I_{i,\min}, I_{i,\max})$.

Although Equation (1) is rather simple, it is readily tailored to different kinds of encounters (Fig. 1). This includes encounters with conspecifics ($i = j$) and individuals of the other species ($i \neq j$). The parameter c_{ij} sets the overall mortality risk. When the other individual is of the same size, $\alpha_{ij} = c_{ij}/2$; mortality increases to a maximum value c_{ij} if the other individual is much larger, and to a minimum of zero if the other individual is much smaller. The term k_{ij} measures the sensitivity of α_{ij} to changes in s_i when $s_i \cong s_j$. The limit as $k_{ij} \rightarrow \infty$ describes a version of the opponent-independent costs game (Parker, 1983), in which the costs arising from an encounter are set prior to the encounter and the larger individual gets all the reward; the costs here would take the form of increased mortality risks inherent from having a larger body size, and the rewards would be reduced mortality risks associated with encounters.

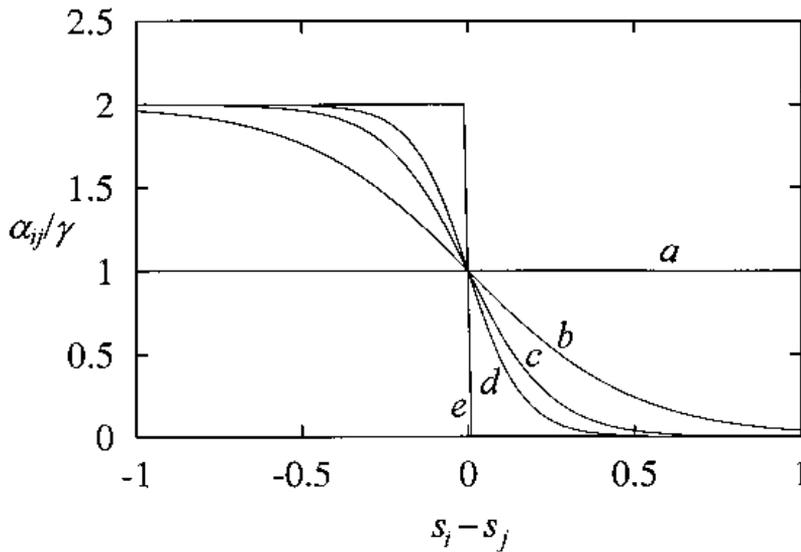


Figure 1. Asymmetric competition functions $\alpha_{ij}(s_i, s_j)$, with $c_{ij} = 2$. (a) No asymmetry: $k_{ij} = 0$; (b) weak asymmetric competition: $k_{ij} = 4$; (c) intermediate asymmetric competition: $k_{ij} = 8$; (d) strong asymmetric competition: $k_{ij} = 12$; (e) the limit as $k_{ij} \rightarrow \infty$.

Population dynamics (mesoscopic scale)

We define a model of population dynamics which describes how the number of individuals in each population is affected by competitive encounters and the fate of mutant individuals with body sizes that differ from those of the residents. By doing this, the need for an external measure of fitness is eliminated; natural selection is described internally by the population dynamics of mutant phenotypes. We start by defining the dynamics of a community without phenotypic variation within species, and then determine the fate of mutants as they are added to it.

Call $s = (s_1, s_2)$ the pair of body sizes in the resident community. Let $n = (n_1, n_2)$ be the number of individuals with each body size at some point in time. With large numbers and the simplest assumption that individuals encounter one another at random, the dynamics are given by:

$$\dot{n}_i = n_i \cdot f_i(s, n) = n_i \cdot \left(\beta_i - \delta_i(s_i) - \sum_{j=1,2} \alpha_{ij}(s_i, s_j) \cdot n_j \right) \quad i = 1, 2 \tag{3}$$

Here the per capita rate of increase, $f_i(s, n)$, is partitioned into the following birth and death components. The first, β_i , is a birth rate; this is taken to be independent of encounters and body size. The second component is a basal rate of mortality, δ_i . The dependence of δ_i on s_i is introduced because an intrinsic cost to large body size is to be expected. We use a linear function

$$\delta_i(s_i) = a_i + b_i s_i \tag{4}$$

to describe this, where a_i and b_i are non-negative parameters. This mortality is augmented by the third component caused by asymmetric competition from Equation (1).

Phenotype evolution (macroscopic scale)

A dynamic for phenotype evolution can be constructed as the mean of a stochastic process, the randomness entering both through mutation and through selection. First we deal with mutation, writing the probability of a mutation per unit time as:

$$\mathcal{M}_i(s'_i, s) = \mu_i \cdot \beta_i \cdot \hat{n}_i(s) \cdot M_i(s'_i - s_i) \quad (5)$$

(Dieckmann and Law, 1996). Here $s'_i = s_i + \delta s_i$ is a mutant phenotype. The term μ_i is the probability that a newborn individual is a mutant. This mutant has a phenotype value drawn from a probability distribution M_i symmetric around s_i and with constant variance σ_i^2 . (Departures from symmetry will have little effect on the deterministic dynamics below, as these are based on the assumption of small mutational steps. A constant variance is most likely when body sizes are log-transformed.) The probability per unit time of a birth is given by the product of the per capita birth probability per unit time, β_i , and the equilibrium population size of the resident phenotypes, $\hat{n}_i(s)$. Equilibrium populations $\hat{n}_i(s)$ are obtained from Equation (3) with $\dot{n}_i = 0$ for $i = 1, 2$. We have made an assumption (A1) in Equation (5) that mutations occur rarely enough for the population sizes to reach equilibrium values between mutation events. This separation of ecological and evolutionary time-scales is widely used in theoretical work, in view of the difficulties in making any generalizations about evolution on the transients of ecological dynamics (e.g. Lande, 1982; Roughgarden, 1983a).

Stochasticity arises during natural selection because mutations occur first in single individuals and are liable to extinction irrespective of how advantageous they are (Fisher, 1958, p. 80 *et seq.*). We now make a second assumption (A2) that populations of residents are large. This has two consequences. First, mutants will initially be rare enough for their effect on the population dynamics of the residents to be ignored. The initial per capita rate of increase of the mutant, $\bar{f}_i(s'_i, s)$, can then be written as a function of the mutant phenotype s'_i and the environment in which it arises, the latter being fully specified by the resident trait values s . Thus:

$$\bar{f}_i(s'_i, s) = \beta_i - \delta_i(s'_i) - \sum_{j=1,2} \alpha_{ij}(s'_i, s_j) \cdot \hat{n}_j(s) \quad (6)$$

This function is related to the fitness generating function (G -function), $G_i(u_i, u, p, N)$, which has been used to characterize evolutionary games in the context of ESS theory, where $u_i = s'_i, u = s, p = (1, 1)$ and $N = \hat{n}$ (Vincent and Brown, 1988; Brown and Vincent, 1992). Rosenzweig and McCord (1991) suggest that the G -function defines a 'bauplan' within which micro-evolution takes place.

The second consequence of assumption (A2) is that the effect of demographic stochasticity on the residents will be negligible. The probability that mutant numbers become large enough to escape extinction due to demographic stochasticity can then be written as:

$$\mathcal{S}_i(s'_i, s) = \begin{cases} \bar{f}_i(s'_i, s) / \beta_i & \text{for } \bar{f}_i(s'_i, s) > 0 \\ 0 & \text{for } \bar{f}_i(s'_i, s) \leq 0 \end{cases} \quad (7)$$

(Goel and Richter-Dyn, 1974, p. 79). With a third assumption (A3) that no two trait values s'_i and s_i can co-exist, a mutant which escapes accidental extinction when rare must go to fixation. Under Lotka-Volterra dynamics, such as those in Equation (3), it can be shown that this assumption typically holds (Dieckmann, 1994, p. 96 *et seq.*).

Assumptions (A1) and (A3) specify a regime which is phenotypically monomorphic except for those times when a mutant is replacing a resident phenotypic value. Under these conditions, the probability per unit time of the transition from s_i to s'_i is given by the product $\mathcal{M}_i(s'_i, s) \cdot \mathcal{S}_i(s'_i, s)$. This is a stochastic mutation–selection process in which, from time to time, new trait values replace old ones in a trait-substitution sequence (Metz *et al.*, 1992). A large number of realizations of this

process can be averaged to give a mean path. As long as the deviations from the mean path are small, the mean path can be replaced by the following deterministic dynamics:

$$\dot{s}_i = \kappa_i(s) \cdot \left. \frac{\partial}{\partial s'_i} \bar{f}_i(s'_i, s) \right|_{s'_i = s_i} \quad \text{for } i = 1, 2 \quad (8)$$

where $\kappa_i(s) = \frac{1}{2} \cdot \mu_i \cdot \sigma_i^2 \cdot \hat{n}_i(s)$ (van Kampen, 1992, p. 122 *et seq.*; Dieckmann and Law, 1996). These dynamics describe the process of phenotypic evolution in a trait space S which is the Cartesian product $S_1 \times S_2$. The dynamics are exact if the mutational steps are infinitesimal and apply as a close approximation if the steps are small – that is, if σ_i^2 is small. Evolution is driven essentially by two factors according to Equation (8). The first is a coefficient $\kappa_i(s)$ that scales the rate of evolution, its value depending on how often mutations occur and the size of the mutational steps. The second is a selection derivative (an evolutionary rate) which depends on the underlying ecological processes responsible for natural selection – that is, what happens when individuals encounter one another and what effect these encounters have on population dynamics. The dynamics are canonical, in that they can alternatively be derived from a starting point in quantitative genetics, although the meaning of the evolutionary rate coefficient is then different (Iwasa *et al.*, 1991; Taper and Case, 1992a; Abrams *et al.*, 1993a; Marrow *et al.*, 1996).

Selection derivative

This measures how sensitive the initial per capita rate of increase of a mutant is to changes in its body size s'_i close to s_i , when the mutant arises in a community with trait values s . It is given by:

$$\left. \frac{\partial}{\partial s'_i} \bar{f}_i(s'_i, s) \right|_{s'_i = s_i} = \lim_{s'_i - s_i \rightarrow 0} \frac{\bar{f}_i(s'_i, s) - \bar{f}_i(s_i, s)}{s'_i - s_i} \quad (9)$$

(Marrow *et al.*, 1992), where $\bar{f}_i(s_i, s) = 0$, since it is assumed that the populations of resident phenotypes have come to equilibrium. The selection derivative is important because it indicates the direction in which evolution is taking place; if it is positive (negative), then mutants of greater (smaller) body size invade. From Equations (1), (4) and (6), it can be written as:

$$\left. \frac{\partial}{\partial s'_i} \bar{f}_i(s'_i, s) \right|_{s'_i = s_i} = \underbrace{-b_i}_{(I)} + \underbrace{\frac{\gamma \cdot c_{ii} \cdot k_{ii}}{4} \cdot \hat{n}_i(s)}_{(II)} + \underbrace{\frac{\gamma \cdot c_{ij} \cdot k_{ij} \cdot u_{ij}(s_i, s_j)}{(1 + u_{ij}(s_i, s_j))^2} \cdot \hat{n}_j(s)}_{(III)} \quad (10)$$

where $u_{ij}(s_i, s_j)$ is as given in Equation (1). This expression comes in three parts: (I) is a constant negative term due to the intrinsic advantage of smaller body size; (II) is a positive term proportional to the number of conspecifics, due to the advantage of larger body size in encounters with these individuals; (III) is also a positive term, in this case due to encounters with individuals of the other species, and proportional to the population size of the other species.

Inner evolutionary isoclines

The isoclines are lines in the trait space S on which $\dot{s}_i = 0$, and are given by the union of the manifolds on which either the resident population or the selection derivative vanishes (Equation 8). We are concerned primarily with the isocline

$$\left. \frac{\partial}{\partial s'_i} \bar{f}_i(s'_i, s) \right|_{s'_i = s_i} = 0 \quad (11)$$

because this allows both species to be present and as a result co-evolution can occur; we call this the *inner* isocline. The following properties of the inner isoclines, which we refer to as *non-invasibility* and *convergence*, help in understanding the phenotype dynamics (see Geritz *et al.*, in press).

Non-invasibility is familiar from the concept of an evolutionarily stable strategy (ESS) as the property that mutants s'_i , with phenotypes close to the isoclinic values s_i satisfying Equation (11), cannot invade (Parker and Maynard Smith, 1990), and is given by the condition:

$$0 > \frac{\partial^2}{\partial s_i^2} \bar{f}_i(s'_i, s) \Big|_{s'_i = s_i} \tag{12}$$

From Equation (10), this condition is:

$$0 > -\gamma \cdot c_{ij} \cdot k_{ij}^2 \cdot \hat{n}_j(s) \cdot u_{ij}(s_i, s_j) \cdot \frac{1 - u_{ij}(s_i, s_j)}{(1 + u_{ij}(s_i, s_j))^3} \tag{13}$$

where $u_{ij}(s_i, s_j)$ is as given in Equation (1). Note that Inequality (13) holds only for the larger species, which means that there is no point in the trait space satisfying it simultaneously for both species.

Convergence was introduced in the context of phenotype dynamics in one dimension and refers to the property of successive mutations in the vicinity of a fixed point to cause evolution towards this point (Taylor, 1989; Abrams *et al.*, 1993a; Metz *et al.*, 1994). This is distinct from the property of non-invasibility and is given by

$$0 > \frac{\partial^2}{\partial s_i \partial s'_i} \bar{f}_i(s'_i, s) \Big|_{s'_i = s_i} + \frac{\partial^2}{\partial s_i^2} \bar{f}_i(s'_i, s) \Big|_{s'_i = s_i} \tag{14}$$

on the inner isocline of this two-dimensional system. Convergence means that, in the vicinity of the isocline, a sequence of successful mutants tends to the isocline, provided that the body size in the other species is held constant.

The fixed points \hat{s} at which both species co-exist are the points in the trait space at which the inner isoclines intersect. That is:

$$\frac{\partial}{\partial s'_i} \bar{f}_i(s'_i, \hat{s}) \Big|_{s'_i = s_i} = 0 \quad \text{for } i = 1, 2 \tag{15}$$

These are of special interest because they are contenders as attractors of evolutionary trajectories; over the course of time, phenotypes may evolve towards them. It is clear from Inequality (13) that, at all fixed points satisfying $\hat{s}_1 \neq \hat{s}_2$, the species with smaller body size is at a fitness minimum, and the one with a greater body size is at a maximum. Nevertheless, it will be seen below that evolution readily leads towards such a point, notwithstanding the fact that it is not an ESS for the species with smaller body size. This is of interest because it shows that the ESS criterion cannot serve as a necessary condition for identifying evolutionary attractors (Brown and Pavlovic, 1992; Abrams *et al.*, 1993a; Marrow *et al.*, 1996). Neither does it qualify as a sufficient condition (Hofbauer and Sigmund, 1990; Takada and Kigami, 1991; Abrams *et al.*, 1993a; Marrow *et al.*, 1996); use of the ESS criterion is inadequate for delimiting the outcome of these evolutionary processes.

Results

The evolutionary dynamics (8) can be represented in terms of a two-dimensional phase portrait in the trait space S . This gives a clear picture of the geometry of evolution, indicating the orientation of the isoclines, the positions of fixed points and the flow of evolutionary trajectories. In this

section, we illustrate the varied evolutionary behaviour which stems from modifications in asymmetric competition in Equation (1) using these phase portraits. Throughout we hold $\gamma = 5 \times 10^{-4}$, $\beta_i = 1$, $a_i = 0$, and $b_i = 1$ for $i = 1,2$ in Equations (1), (3) and (4), as this makes it possible to focus simply on the effects of changes to asymmetric competition. The coefficients of the evolutionary rates of the species in Equation (8) are kept the same unless otherwise stated.

It is important to appreciate that, on the time-scale of population dynamics, the species may not co-exist; that is, the asymptotic state to which the population size of one species tends may be zero for constant s . To make this precise, we define a subspace S_c of S for which both species have positive equilibrium populations asymptotically:

$$S_c = \{s \in S \mid \hat{n}_i(s) > 0 \text{ for } i = 1,2\} \tag{16}$$

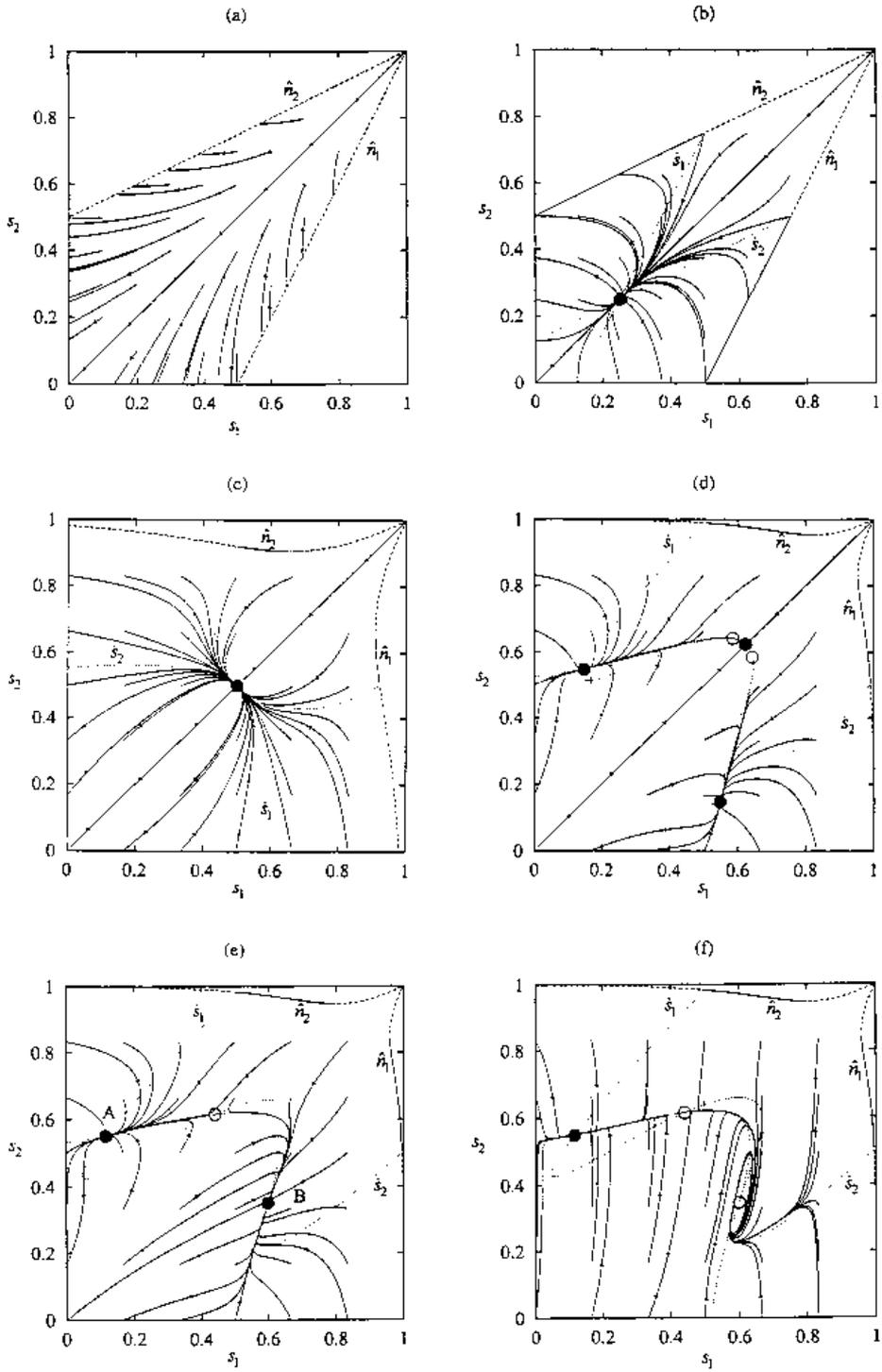
It may often be the case that S_c is an empty set, and questions about co-evolution obviously do not then arise. We deal here only with those systems for which S_c is not empty, so that there is some region in which co-evolution takes place. For this to be the case, we require that there should be some region in S with the properties:

$$\frac{\beta_i - \delta_i(s_i)}{\alpha_{ii}(s_i, s_i)} < \frac{\beta_j - \delta_j(s_j)}{\alpha_{ji}(s_j, s_i)} \text{ for } i = 1,2 \text{ and } j \neq i \tag{17}$$

These conditions ensure that there is an equilibrium point satisfying $\hat{n}_i(s) > 0$ for $i = 1,2$, and that the equilibrium point is a global attractor. With the values β_i , a_i and b_i given above, there are values of s satisfying Inequality (17) when $c_{ii} > c_{ji}$ for $i = 1,2$ and $j \neq i$. This is no more than saying that there is a region in S where intraspecific competition is stronger than interspecific competition. To ensure that there is a substantial region of co-existence, we set $c_{ii} = 2$ and $c_{ij} = 1$ for $i = 1,2$ and $j \neq i$ in the examples below.

Note that, once evolution of body size has been introduced, it is entirely feasible for the body sizes to evolve to the boundary of the subspace of co-existence S_c – that is, to a point where the equilibrium population size of one of the species is zero. In such cases, the dynamics subsequently lie in one of the one-dimensional subspaces S_1 or S_2 . We indicate such parts of the S_c boundary by discontinuous lines in Fig. 2, in contrast to those which repel the evolutionary trajectories. It should be borne in mind that the deterministic population dynamics in Equation (3) do not allow for accidental extinction of a species close to the S_c boundary that results from the small size of the resident population there.

Figure 2. Phase portraits of the trait space S , showing contrasting dynamics as asymmetric competition is altered. Evolutionary trajectories within the region of co-existence shown as continuous lines. Inner evolutionary isoclines $\dot{s}_i = 0$ shown as dotted lines: \dot{s}_1 species 1, \dot{s}_2 species 2. Isoclines marking the boundary of co-existence $\hat{n}_i = 0$ shown as: \hat{n}_1 species 1, \hat{n}_2 species 2; the isocline is given as continuous (discontinuous) if it repels (attracts) orbits from the interior of the co-existence region. Fixed points are shown as circles (○) and as filled circles (●) if the fixed point is an attractor. Parameters are set as follows unless otherwise specified: Equation (1): $\gamma = 5 \times 10^{-4}$, $c_{ii} = 2$, $c_{ij} = 1$, $k_{ii} = 4$, for $i = 1,2$ and $j \neq i$; Equation (3): $\beta_i = 1$, for $i = 1,2$; Equation (4): $a_i = 0$, $b_i = 1$, for $i = 1,2$; Equation (8): $\mu_i = 10^{-4}$, $\sigma_i^2 = 10^{-6}$, for $i = 1,2$. (a) No asymmetric competition within and between species: $k_{ij} = 0$, for $i,j = 1,2$. (b) Asymmetric competition present within species and absent between species: $k_{12} = 0$, $k_{21} = 0$. (c) Moderate asymmetric competition between species: $k_{12} = 4$, $k_{21} = 4$. (d) Strong asymmetric competition between species: $k_{12} = 8$, $k_{21} = 8$. (e) Differences between species in interspecific asymmetric competition functions: $k_{12} = 9$, $k_{21} = 7$. (f) Differences between species in interspecific asymmetric competition functions together with fast evolutionary rate for species 2: $k_{12} = 9$, $k_{21} = 7$, $\sigma_2^2 = 10^{-5}$.



Asymmetry absent

This is the null case, indicating what would happen if competition was present but there were no asymmetries in the encounters ($c_{ij} > 0$, $k_{ij} = 0$ for $i, j = 1, 2$). The path of evolution is very simple (Fig. 2a): body sizes just evolve to the smallest values in S . This is because the intrinsic costs associated with large size (Equation 4) are not countered by any advantage in encounters with other individuals. Note that, in certain regions of the trait space S , co-existence is not possible; body size, if large enough, causes an intrinsic mortality rate too great to maintain a population under competition. Moreover, evolution can lead to the boundary of S_c , and there the larger species becomes extinct. Evolution then continues in one of the subspaces S_1, S_2 until the smallest body size is reached.

Asymmetric competition within species

A first step towards a more realistic system would be to suppose that asymmetric encounters occur only among conspecifics ($k_{ii} > 0$, $k_{ij} = 0$ for $i = 1, 2$ and $i \neq j$). This would be expected if asymmetries were a special feature of intraspecific interactions, such as the ability to hold territories against conspecifics (Davies, 1978). Figure 2b shows that the intrinsic advantage of small size is now opposed by an advantage of larger body size in encounters with conspecifics. Just how great the overall advantage stemming from asymmetric encounters is depends on the number of conspecifics (Equation 10). When conspecifics are scarce, as they will be when body size is large, encounters occur infrequently and the advantage is not great enough to counter that of small body size. This is reversed when body size is small and, as a result, inner evolutionary isoclines exist for both species. The isoclines intersect at a single point \hat{s} , which satisfies the condition for convergence for both species and the second-order condition for non-invasibility for neither of them (see Inequalities 13 and 14); nonetheless, it is an attractor for evolutionary trajectories in its neighbourhood. As before, evolution leads to the boundary of S_c from certain starting points, although this can now happen only over a subset of the boundary.

Moderate asymmetric competition between species

Asymmetric competition between species, in addition to that within species, is likely to occur when all individuals must compete for a common resource, irrespective of their identity. This changes some important features of the phase portrait. We consider first a case in which the degree of asymmetry is equal for both species ($k_{12} = k_{21}$) and moderate in size (Fig. 2c). The inner isoclines and the boundary of S_c are now non-linear. In the example shown, the single fixed point, now shifted to larger body sizes, still remains in existence and is still an attractor for evolutionary trajectories in its neighbourhood. It is notable that the asymmetry in interspecific encounters expands the region S_c over which the species co-exist. This may seem counterintuitive until it is understood that individuals of large body size are now less adversely affected in their encounters with small individuals of the other species and that their populations are correspondingly larger. A substantial part of the non-linear boundary of S_c permits evolution on to the boundary, leading to extinction of the larger species.

Strong asymmetric competition between species

As the asymmetry between species is made stronger, the non-linearities of the inner isoclines become greater, generating more fixed points. This is because, where individuals of the two species are similar in size, the advantage of being the larger one becomes greater; this distorts the inner isoclines, pulling them towards the upper right corner, $s = (1, 1)$. In Fig. 2d, for example, the single

fixed point has been replaced by five fixed points. The one in the middle at which the species have the same body size still exists and has a small basin of attraction. But two new attracting fixed points have arisen at which the body sizes of the two species are quite different; these are attractors even though the species with smaller body size is at a fitness minimum (see Inequality 13). Evidently, as the degree of asymmetry increases, alternative outcomes to co-evolution become possible; which outcome is realized depends on the body sizes at the start of the evolutionary process.

Differences in interspecific asymmetric competition

In general, the advantage gained by a large individual of species 1 over a small individual of species 2 does not have to be the same as the advantage to an individual of species 2 when the sizes are reversed ($k_{12} \neq k_{21}$). For instance, one might well expect the canopy architecture of two plant species to differ; the one with the more open canopy then has a less adverse effect on its smaller neighbours than the species with the more closed canopy when there is competition for light. Such differences between species seem particularly likely when the species in competition are not closely related (Englund *et al.*, 1992).

Differences in the degree of asymmetry between species can add further complexities to the dynamics, because the phase portrait is no longer symmetric about the line $s_1 = s_2$. Figure 2e gives an example in which the inner isoclines intersect at three points, the outer two points (A) and (B) both being attractors. Fixed point (A) satisfies the condition for convergence for both species and the condition for non-invasibility for species 2 (Inequalities 13 and 14). Point (B) satisfies the conditions for non-invasibility and convergence for species 1 only. This illustrates the fact that convergence by both species is not necessary for the fixed point to be an attractor, just as non-invasibility is not (Abrams *et al.*, 1993a; Marrow *et al.*, 1996).

In fact, the stability properties of fixed point (B) depend on the coefficients that scale the evolutionary rates in Equation (8), in addition to the properties of the inner isoclines. This is shown in Fig. 2f, where the coefficient of species 2 is increased by a factor of 10. As can be seen from the orientation of the trajectories, evolution in the vertical direction (species 2) is now faster than in the horizontal direction (species 1), and this prevents point (B) from being an attractor. The evolutionary trajectories are nonetheless confined to a region around the fixed point, and consequently the asymptotic state is now a periodic orbit.

The periodic asymptotic state constitutes a 'Red Queen' dynamic, the sequence of trait substitutions continuing for as long as the system remains in existence (Fig. 3a) (Marrow *et al.*, 1992, 1996; Dieckmann *et al.*, 1995). Depending on where the species are on the periodic orbit, invasions are sometimes by larger mutants, and sometimes by smaller mutants. The oscillations in body size of the two species are nearly in phase, but the larger evolutionary rate constant of species 2 causes it to have oscillations of greater amplitude. The cycle cannot be driven by changes in the relative abundance of the two species (cf. Pimentel, 1968; Pease, 1984), since their equilibrium numbers are approximately in phase, being high when body size is relatively small (Fig. 3b). Selection follows these changes in population size, the component due to intraspecific encounters being at its peak when numbers are greatest, as measured by Equation (10) part (II) (Fig. 3c). Conversely, the component due to interspecific encounters is at its peak when the numbers are lowest, as measured by Equation (10) part (III).

Discussion

The results above show that asymmetric competition between species can, in principle, have the following evolutionary effects. First, the non-linearities in the inner isoclines created by asymmetric

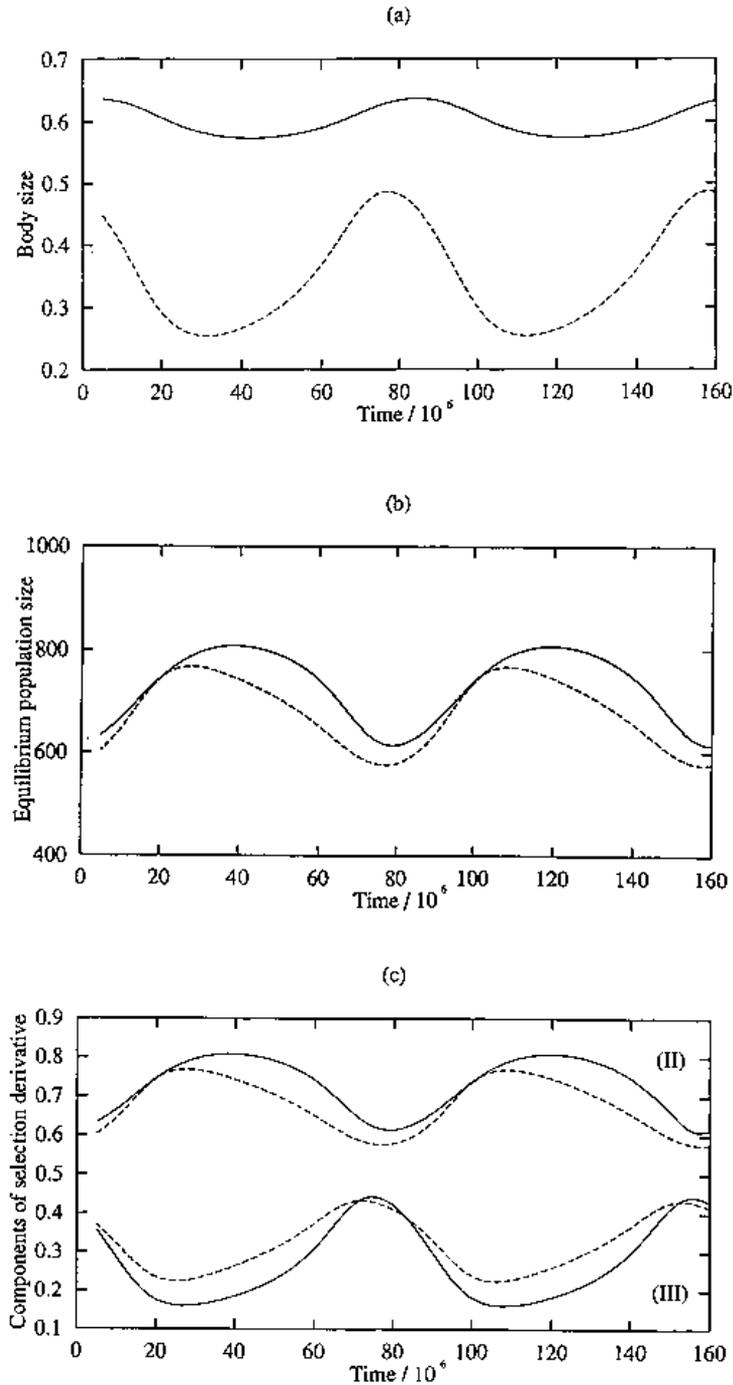


Figure 3. Properties of the periodic attractor of Fig. 2f, the variables being given as functions of time: (a) body size; (b) equilibrium population size/ (2×10^3) ; (c) the intraspecific component of the selection derivative (Equation 10II) shown as II, and the interspecific component of the selection derivative (Equation 10III) shown as III. Continuous lines: species 1; discontinuous lines: species 2. Parameter values as in Fig. 2f.

competition (a) cause evolutionary fixed points to be shifted to larger body sizes, and (b) can give rise to multiple fixed points. Second, the asymptotic states can be periodic orbits (Red Queen dynamics), rather than fixed points. Third, because large individuals suffer less disadvantage when competition is asymmetric, co-existence of the species occurs over a larger part of the phenotype space. Fourth, evolution to the boundary of the co-existence region remains possible, and the smaller species then drives the larger one to extinction, as Taper and Case (1992a) found in their analysis. Much of this rich behaviour arises from modelling evolution in a manner that links it directly to the underlying population dynamics. Such population processes are important for ecologically significant traits, because the selection pressures one species generates upon another depend on the abundance of the species concerned, as is clear from Equation (10) (see also Pimentel, 1968; Abrams and Matsuda, 1994).

Quasi-monomorphism

To lay bare the links from individual encounters, through population dynamics, to a macroscopic model of co-evolution, we have deliberately kept the processes operating at each scale rather simple. As a result, some warnings about the limitations of the phenotype dynamics in Equation (8) are needed. The most critical assumption is that the populations can be treated, to a good approximation, as monomorphic with respect to the evolving traits. Clearly, one would wish to remove this; a model which tracks phenotype distributions through time would be preferable. The quantitative-genetic recursion used by Slatkin (1980) and Taper and Case (1985, 1992a) does retain the phenotype distribution, but does not deal with the mutation process and is much less tractable analytically. What we know from our stochastic simulations is that the model remains a good approximation to the mean of a stochastic birth–death process in which different phenotypes occur with a low probability through mutation, generating a phenotype distribution with a small variance (Dieckmann, 1994; Dieckmann *et al.*, 1995).

The assumption of almost complete monomorphism is widely made in modelling co-evolution, through the use of the first-order term of a Taylor's expansion of the fitness function (i.e. a selection derivative of the form used in Equation 8). In models motivated by quantitative genetics, the argument of the function is the additive genetic value, in which case monomorphism applies to this rather than the phenotypic value (Iwasa *et al.*, 1991; Taper and Case, 1992a; Abrams *et al.*, 1993a; Marrow *et al.*, 1996). One might alternatively require that terms in the fitness function of order greater than 2 are negligible (Abrams *et al.*, 1993b), but this would not be generic for co-evolving systems. Dynamics like those of Equation (8) have been used heuristically on a number of occasions in evolutionary biology (e.g. Brown and Vincent, 1987; Hofbauer and Sigmund, 1990); these approaches also have an assumption of monomorphism, although this is not made explicit.

Dynamical systems and evolutionary game theory

The model illustrates how dynamical and game-theoretic approaches to the study of evolution differ. Game-theoretic approaches use isoclinic properties of non-invasibility (the ESS condition). But it is clear from the phase portraits that this isoclinic property is not enough to indicate whether the fixed point is an attractor of the evolutionary trajectories (Takada and Kigami, 1991; Abrams *et al.*, 1993a; Marrow *et al.*, 1996). In addition, they can provide no information on periodic attractors, where the trajectories do not tend to a fixed point at all. There appears to be no shortcut; direct investigation of the dynamical system is needed.

Nevertheless, the isoclinic properties do provide some useful insights. For instance, in the co-evolutionary system considered here, at any fixed point with the property $\hat{s}_1 \neq \hat{s}_2$, the species with

smaller body size is at a fitness minimum. Although selection on the larger species is stabilizing, it is disruptive for the smaller one and this may lead to a polymorphism developing (Christiansen, 1991; Metz *et al.*, 1994; Geritz *et al.*, in press). In this event, evolutionary branching takes place, and the quasi-monomorphic evolutionary dynamic we have used is no longer appropriate. In principle, it is possible to follow the evolution further, by increasing the dimensionality of Equation (8) to three, and treating the two phenotypes of the smaller species separately. We have not done this because theoretical results, as well as stochastic simulations, demonstrate that the time-scale of evolutionary branching is beyond that of quasi-monomorphic co-evolutionary change for our model.

Genetic systems

Strictly speaking, the model we have described applies only to phenotypes with an asexual or haploid genetic system. We suggest that, with few modifications, the dynamics would also apply over much of the trait space to a diploid genetic system if there is an ordering of the phenotypic effects of the genes. The ordering is either that $s_i < s'_i < s''_i$ or that $s_i > s'_i > s''_i$, where s'_i and s''_i are the phenotypes of the mutant heterozygote and homozygote respectively; additivity of the phenotypic effects is a special case of this. The probability that a mutant replaces a resident allele depends first of all on the probability that it escapes extinction when rare; this is still given by Equations (6) and (7), the per capita rate of increase now being that of the rare heterozygote. Replacement subsequently depends on whether the mutant goes to fixation. As long as s_i and s'_i do not straddle the inner s_i -isocline, this ordering should lead to fixation of mutants which have escaped extinction when rare. Moreover, polymorphisms straddling the isocline would not normally be maintained, because evolution in the other species usually moves the system away from the vicinity of the isocline. Exceptions to this are the evolutionary fixed points themselves; here the larger species may go into a sustained polymorphic state, in which case the assumption of quasi-monomorphism no longer applies. Note that the evolutionary rate coefficient in Equation (8) has to be multiplied by a factor of two if a switch from haploidy to diploidy is involved.

Transients of evolutionary dynamics

The focus of most early work on evolution of competing species was the divergence of characters, in view of the potential importance of niche differentiation in structuring ecological communities (Hutchinson, 1959; Roughgarden, 1983b). The trajectories in Fig. 2 illustrate how minor a role character divergence can play once asymmetric competition is introduced (see also Abrams, 1987; Taper and Case, 1992a). Character divergence would require a region in the phase space where the species with larger body size evolves still larger sizes and the smaller species evolves still smaller sizes. Although such regions do exist, the dynamics over most of the phase space comprise either character convergence or parallel character shifts (Taper and Case, 1992b). Convergence occurs when the larger species is evolving to a smaller size and the smaller one to a larger size, as in the top left and bottom right regions of the phase space. Parallel character shifts occur when both species change in the same direction, as in most of the rest of the phase space. The parallel character shifts may themselves be convergent, getting closer to the line $s_1 = s_2$, but it is also common in our examples to observe divergent shifts, getting further away from the line $s_1 = s_2$. Note that, if there had already been single-species evolution to a fixed point before the two species met, the starting point for co-evolution would be the body size at the fixed point that applies in the absence of interspecific competition.

Red Queen dynamics

The results show that evolution can lead to a cyclic asymptotic state, although our exploration of the parameter space suggests that such behaviour is relatively infrequent. The existence of a Red Queen dynamic is important for several reasons. First, it warns that the current preoccupation of evolutionary theory with fixed-point asymptotic states of evolution, in particular ESSs, misses other possible outcomes (Dieckmann *et al.*, 1995); these are likely to require more consideration as theorists turn to problems of higher dimensionality, such as those of co-evolution. Second, it demonstrates that continuing evolution is not dependent on changes in the abiotic environment (although normally this obviously plays a major part); all that is needed is a system of interacting and mutating species to prevent evolution from coming to a halt.

Cyclic solutions are well known from previous studies of evolution under asymmetric competition within species. What happens is that mutants with body sizes greater than those prevailing in the population gain an advantage and body size increases; but eventually mutants of small size can invade because they gain an advantage so great from the low costs of small size that this outweighs the defeat they experience in every encounter (Maynard Smith and Brown, 1986). Such models have the properties that: (a) mutants can cause large changes in phenotype, and (b) the pay-offs are discontinuous functions of phenotype. Parker (1985) suggested that cyclic systems will typically revert to fixed-point behaviour if the pay-offs are made continuous; if, in addition, mutational steps are made small, cyclic dynamics ought to become still less likely. That Red Queen dynamics can still occur in our model, under a small mutation variance and a continuous fitness function, suggests that cyclic asymptotic states to phenotypic evolution are more robust than has previously been thought.

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References

- Abrams, P.A. (1987) Alternative models of character displacement and niche shift. 2. Displacement when there is competition for a single resource. *Am. Nat.* **130**, 271–282.
- Abrams, P.A. and Matsuda, H. (1994) The evolution of traits that determine ability in competitive contests. *Evol. Ecol.* **8**, 667–686.
- Abrams, P.A., Matsuda, H. and Harada, Y. (1993a) Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.* **7**, 465–487.
- Abrams, P.A., Harada, Y. and Matsuda, H. (1993b) On the relationship between quantitative genetic and ESS models. *Evolution* **47**, 877–887.
- Brown, J.S. and Pavlovic, N.B. (1992) Evolution in heterogeneous environments: Effects of migration on habitat specialization. *Evol. Ecol.* **6**, 260–382.
- Brown, J.S. and Vincent, T.L. (1987) Coevolution as an evolutionary game. *Evolution* **41**, 66–79.
- Brown, J.S. and Vincent, T.L. (1992) Organization of predator–prey communities as an evolutionary game. *Evolution* **46**, 1269–1283.
- Case, T.J. and Bolger, D.T. (1991) The role of interspecific competition in the biogeography of island lizards. *Trends Ecol. Evol.* **6**, 135–139.
- Christiansen, F.B. (1991) On the conditions for evolutionary stability for a continuously varying character. *Am. Nat.* **138**, 37–50.

- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M. and Guinness, F.E. (1979) The logical stag: Aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* **27**, 211–275.
- Connell, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35**, 131–138.
- Connell, J.H. (1983) On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *Am. Nat.* **122**, 661–696.
- Davies, N.B. (1978) Territorial defence in the speckled wood butterfly (*Pararge aegeria*): The resident always wins. *Anim. Behav.* **26**, 138–147.
- Dieckmann, U. (1994) *Coevolutionary Dynamics of Stochastic Replicator Systems*. Berichte des Forschungszentrums Jülich (Jül-3018), Jülich, Germany.
- Dieckmann, U. and Law, R. (1996) The dynamical theory of coevolution: A derivation from stochastic ecological processes. *J. Math. Biol.* **34**, 579–612.
- Dieckmann, U., Marrow, P. and Law, R. (1995) Evolutionary cycling in predator–prey interactions: Population dynamics and the Red Queen. *J. Theor. Biol.* **176**, 91–102.
- Englund, C., Johansson, F. and Olsson, T.I. (1992) Asymmetric competition between different taxa: Poeciliid fishes and water striders. *Oecologia* **92**, 498–502.
- Fisher, R.A. (1958) *The Genetical Theory of Natural Selection*, 2nd edn. Dover Publications, New York.
- Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. (in press) Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*
- Goel, N.S. and Richter-Dyn, N. (1974) *Stochastic Models in Biology*. Academic Press, New York.
- Goldberg, D.E. (1987) Neighbourhood competition in an old-field plant community. *Ecology* **68**, 1211–1223.
- Hofbauer, J. and Sigmund, K. (1990) Adaptive dynamics and evolutionary stability. *Appl. Math. Lett.* **3**, 75–79.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals. *Am. Nat.* **93**, 145–159.
- Iwasa, Y., Pomiankowski, A. and Nee, S. (1991) The evolution of costly mate preferences. II. The ‘handicap’ principle. *Evolution* **45**, 1431–1442.
- Lande, R. (1982) A quantitative genetic theory of life history evolution. *Ecology* **63**, 607–615.
- Lawton, J.H. and Hassell, M.P. (1981) Asymmetrical competition in insects. *Nature* **289**, 793–795.
- Marrow, P., Law, R. and Cannings, C. (1992) The coevolution of predator–prey interactions: ESSs and Red Queen dynamics. *Proc. R. Soc. Lond. B* **250**, 133–141.
- Marrow, P., Dieckmann, U. and Law, R. (1996) Evolutionary dynamics of predator–prey systems: An ecological perspective. *J. Math. Biol.* **34**, 556–578.
- Matsuda, H. and Abrams, P.A. (1994) Runaway selection to self-extinction under asymmetrical competition. *Evolution* **48**, 1764–1772.
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Maynard Smith, J. and Brown, R.L. (1986) Competition and body size. *Theor. Pop. Biol.* **30**, 166–179.
- Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. (1992) How should we define ‘fitness’ for general ecological scenarios? *Trends Ecol. Evol.* **7**, 198–202.
- Metz, J.A.J., Geritz, S. and Iwasa, Y. (1994) *On the Classification of Evolutionarily Singular Strategies*. University of Leiden Preprint, Leiden, The Netherlands.
- Morin, C. and Johnson, E.A. (1988) Experimental studies of asymmetric competition among anurans. *Oikos* **53**, 398–407.
- Parker, G.A. (1983) Arms races in evolution – an ESS to the opponent-independent costs game. *J. Theor. Biol.* **101**, 619–648.
- Parker, G.A. (1985) Population consequences of evolutionarily stable strategies. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (R.M. Sibly and R.H. Smith, eds), pp. 33–58. Blackwell Scientific, Oxford.
- Parker, G.A. and Maynard Smith, J. (1990) Optimality theory in evolutionary biology. *Nature Lond.* **348**, 27–33.
- Pease, C.M. (1984) On the evolutionary reversal of competitive dominance. *Evolution* **38**, 1099–1115.

- Perfecto, I. (1994) Foraging behaviour as a determinant of asymmetric competitive interaction between two ant species in a tropical ecosystem. *Oecologia* **98**, 184–192.
- Pimentel, D. (1968) Population regulation and genetic feedback. *Science* **159**, 1432–1437.
- Robinson, S.K. and Terborgh, J. (1995) Interspecific aggression and habitat selection by Amazonian birds. *J. Anim. Ecol.* **64**, 1–11.
- Rosenzweig, M.L. and McCord, R.D. (1991) Incumbent replacement: Evidence for long-term evolutionary progress. *Paleobiology* **17**, 202–213.
- Roughgarden, J. (1983a) The theory of coevolution. In *Coevolution* (D.J. Futuyma and M. Slatkin, eds), pp. 33–64. Sinauer Associates, Sunderland, MA.
- Roughgarden, J. (1983b) Coevolution between competitors. In *Coevolution* (D.J. Futuyma and M. Slatkin, eds), pp. 383–403. Sinauer Associates, Sunderland, MA.
- Roughgarden, J.D. and Pacala, S.W. (1989) Taxon cycle among *Anolis* lizard populations: Review of the evidence. In *Speciation and Its Consequences* (D. Otte and J.A. Endler, eds), pp. 403–432. Sinauer Associates, Sunderland, MA.
- Rummell, J.D. and Roughgarden, J. (1983) Some differences between invasion-structured and coevolution-structured competitive communities: A preliminary theoretical analysis. *Oikos* **41**, 477–486.
- Rummell, J.D. and Roughgarden, J. (1985) A theory of faunal buildup for competition communities. *Evolution* **39**, 1009–1033.
- Schoener, T.W. (1983) Field experiments on interspecific competition. *Am. Nat.* **122**, 240–285.
- Schwinning, S. and Fox, G.A. (1995) Population dynamic consequences of competitive symmetry in annual plants. *Oikos* **72**, 422–432.
- Slatkin, M. (1980) Ecological character displacement. *Ecology* **61**, 163–177.
- Takada, T. and Kigami, J. (1991) The dynamical attainability of ESS in evolutionary games. *J. Math. Biol.* **29**, 513–529.
- Taper, M.L. and Case, T.J. (1985) Quantitative genetic models for the coevolution of character displacement. *Ecology* **66**, 355–371.
- Taper, M.L. and Case, T.J. (1992a) Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* **46**, 317–333.
- Taper, M.L. and Case, T.J. (1992b) Coevolution among competitors. In *Oxford Surveys in Evolutionary Biology*, Vol. 8 (D.J. Futuyma and J. Antonovics, eds), pp. 63–109. Oxford University Press, Oxford.
- Taylor, P.D. (1989) Evolutionary stability in one parameter models under weak selection. *Theor. Pop. Biol.* **36**, 125–143.
- Thompson, P. and Fox, B.J. (1993) Asymmetric competition in Australian heathland rodents: A reciprocal removal experiment demonstrating the influence of size-class structure. *Oikos* **67**, 264–278.
- van Kampen, N.G. (1992) *Stochastic Processes in Physics and Chemistry*. North-Holland, Amsterdam.
- Van Valen, L. (1973) A new evolutionary law. *Evol. Theory* **1**, 1–30.
- Vincent, T.L. and Brown, J.S. (1988) The evolution of ESS theory. *Ann. Rev. Ecol. Syst.* **19**, 423–443.
- Weiner, J. (1990) Asymmetric competition in plant populations. *Trends Ecol. Evol.* **5**, 360–364.