Working Paper

Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective

Paul Marrow, Ulf Dieckmann, and Richard Law

WP-96-02
March 1996

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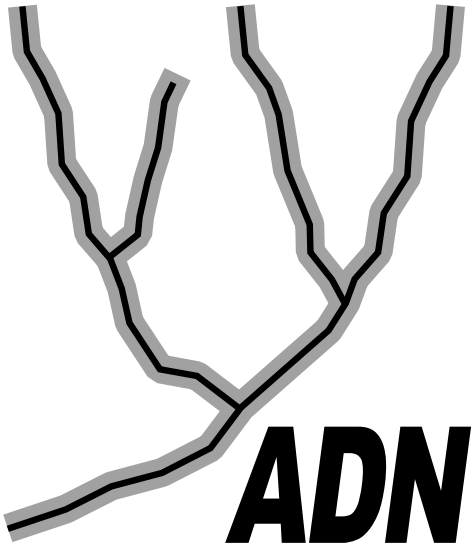

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Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective

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Evolution takes place in an ecological setting that typically involves interactions with other organisms. To describe such evolution, a structure is needed which incorporates the simultaneous evolution of interacting species. Here a formal framework for this purpose is suggested, extending from the microscopic interactions between individuals — the immediate cause of natural selection, through the mesoscopic population dynamics responsible for driving the replacement of one mutant phenotype by another, to the macroscopic process of phenotypic evolution arising from many such substitutions. The process of coevolution that results from this is illustrated in the context of predator-prey systems. With no more than qualitative information about the evolutionary dynamics, some basic properties of predator-prey coevolution become evident. More detailed understanding requires specification of an evolutionary dynamic; two models for this purpose are outlined, one from our own research on a stochastic process of mutaton and selection and the other from quantitative genetics. Much of the interest in coevolution has been to characterize the properties of fixed points at which there is no further phenotypic evolution. Stability analysis of the fixed points of evolutionary dynamical systems is reviewed and leads to conclusions about the asymptotic states of evolution rather different from those of game-theoretic methods. These differences become especially important when evolution involves more than one species.

1 Introduction

It is a central problem in evolutionary theory that the evolution of a lineage needs to be considered in the context of ecological conditions experienced by the lineage. Natural selection, the source of much biotic evolution, is driven by differences among organisms in survival and reproduction as they live out their lives in an ecological setting, and the relationship between evolution and ecology is aptly summed up in Hutchinson's (1967) metaphor 'The ecological theater and the evolutionary play'. The birth and death processes of individuals are a common object of study of both subjects, and there

is a wide recognition that a synthesis of the relevant areas of population ecology and evolutionary genetics is needed to inject an ecological basis into evolutionary theory; see for instance comments by Lewontin (1979).

The ecological setting of evolution can take many different forms, involving abiotic as well as biotic factors. In this paper we focus on the ecological process of predation, and consider how to model the evolutionary dynamics generated by an interaction between a prey and predator species. We do this to provide some background to the subject for theoreticians interested in entering the subject area, and also to illustrate and place in context some mathematical methods developed by Marrow et al. (1992) and Dieckmann and Law (1996). Although we concentrate on predation, the main ideas can be applied to a variety of biotic interactions falling within the scope of *coevolution*, a term coined by Ehrlich and Raven (1964) to describe the evolutionary process caused by the coupled evolution of all of the lineages concerned. Slatkin and Maynard Smith (1979) and Futuyma and Slatkin (1983) give introductions to coevolution. In a coevolving system, the evolution of the component species needs to be considered simultaneously, because evolutionary changes in one species can be the cause of evolutionary changes in the other(s).

A number of biological issues are raised by the coevolution of predators and prey. Most important is an instability inherent in their coevolution, since natural selection by the prey on the predator favours predator phenotypes best able to consume the prey, whereas selection by the predator on the prey favours prey phenotypes least likely to be killed. This may lead to an escalation in traits affecting attack and defence, referred to as an evolutionary 'rat race' by Rosenzweig (1973) and an 'arms race' by Dawkins and Krebs (1979). Abrams (1986) argued that an arms race does not exhaust the possibilities; for example, continuing evolution in one species may occur even if the other remains constant. Although evidence is hard to find, Bakker (1983) documented changes in mammalian herbivores and carnivores during the Paleocene to Mid Eocene that could be of the kind suggested by Dawkins and Krebs (1979). Those taxa characteristic of open habitats, where pursuit and flight are critical features of predation, show similar speed-enhancing changes in limb morphology; during this time the prey appear to have evolved faster than predators. Dawkins and Krebs (1979) argued that an asymmetry in the selection pressures would be expected, on the grounds that the prey is running for its life whereas the predator 'is only running for his dinner'. Notice that, if the predator evolves faster than the prey, it could gain such a great advantage that it destroys its prey altogether and brings about its own extinction. This led for example Slobodkin (1968, 1974) and Michod (1979) to consider how the apparent 'prudence' in exploitation of prey by natural predators could come about by selection operating at the level of the individual. One likely cause is that the predator selects for prey life histories in

which the effects of predation on the prey's reproductive success are reduced, a process experimentally confirmed in the water flea *Daphnia magna* by Edley and Law (1988).

To investigate these and other issues arising in the coevolution of predators and prey it helps to have a formal structure for modelling the process. Such models might be cast in terms of population genetics, evolutionary game theory, or quantitative genetics. Population genetics deals with how the frequency of a gene in each species with some effect on the interaction changes over the course of time, as discussed by Jayakar and Zonta (1990). This approach is to focus on the detailed dynamics of single genes. Evolutionary game theory in contrast sacrifices genetics to focus on the details of ecological, frequency-dependent interactions among organisms. Each species is assumed to comprise a set of phenotypes influencing the interaction, and a search is made for fixed points at which the phenotypes present are uninvadable by others; see for instance Parker (1983, 1985). The focus in this case is on an endpoint of evolution and, implicit in this, is an assumption that a sequence of gene substitutions, the stuff of population genetics, can bring the system to the fixed point in the first place. With these two approaches in mind, evolution has been likened to the motion of a streetcar, with many stops and starts as one gene is substituted for another, before eventually reaching the terminus; population genetics deals with the path between one stop and the next, and evolutionary game theory searches for the terminus. (We will see below, however, that a terminus does not necessarily exist.) The third approach, quantitative genetics, focuses on statistical properties of traits with continuous variation caused by the environment and a large (unspecified) number of genes with small effects; see for example Saloniemi (1993). This has the advantage that many of the traits important in coevolution are continuous variables, and the disadvantage that, like much of evolutionary game theory, it lacks an explicit mechanistic basis in genetics.

The approach used here is motivated by the ecology of interactions between predators and prey-the proximate cause of natural selection. The evolutionary variables are therefore phenotypic traits (properties such as body weight or height) rather than gene frequencies. But we wish to go beyond the game theoretic study of fixed points to investigate a dynamical system of evolution within which the properties of fixed points can be seen in their proper context. This could be done either through quantitative genetics or as a development of evolutionary game theory; we have chosen the latter path to keep a close connection with game theory. Casting the dynamics in these terms entails some compromise over the genetic system; the methods we describe apply explicitly to a system of pure-breeding clones, but it will be seen that a model used in quantitative genetics has many of the same features. Our approach also departs from single-species evolutionary game theory in being based on density in addition to frequency of different phenotypes. This is an important ecological feature when dealing

with games between species because, as Pimentel (1968) pointed out, the whole game achieves more or less significance in the evolution of each species as the abundance of the other species becomes respectively greater or lower.

2 A Structure for Modelling Coevolution

We seek a formal description for the process of coevolution that works from the details of phenotype-dependent interactions of individuals (the cause of natural selection) to the large-scale phenotypic evolution of the system. One would like the process to be 'self-referencing' in the sense that the path of evolution is driven internally by the population dynamics of the interacting species. We focus on one prey and one predator species, but note that the structure could readily be extended to systems with greater numbers of species and involving other kinds of interactions, as described by Dieckmann (1994) and Dieckmann and Law (1996). The following argument rests on a hierarchy of three time scales: microscopic interactions among individuals, mesoscopic population dynamics, and macroscopic phenotypic evolution.

2.1 Interactions among Individuals

Suppose that coevolution is taking place in one trait in each species, the value of the trait in an individual (i.e. its phenotype) being s_1 in the prey and s_2 in the predator; the traits might for instance be adult body sizes. The trait values are taken to be continuous and are elements of the sets S_1 and S_2 in the prey and predator respectively. The phenotypes of a prey individual and a predator individual, which are denoted $s = (s_1, s_2)$ and taken from the set $S = S_1 \times S_2$, determine what happens when they encounter one another. One must specify the effect of the encounter on the birth and death rates of the individuals concerned. In qualitative terms the encounter will most likely lead to an increased risk of mortality in the prey; the predator on the other hand most likely experiences a reduced rate of mortality or, in the longer term, an increased rate of reproduction, or both. How great the effect on the vital rates is, depends on the phenotypes of the individuals; any difference in vital rates between co-occuring conspecific individuals with different phenotypes causes natural selection. For instance, a large prey individual is more likely than a small one to defend itself successfully from a predator of intermediate size and, as a result, to gain a selective advantage through a lower risk of death in the encounter. Some specific choices for the effect of encounters on vital rates are given in an example in Section 3.

2.2 Population Dynamics of Resident Phenotypes

The population dynamics described below will drive the replacement of one phenotype by another. Suppose first, as a preliminary, that each species comprises only one phenotype, the pair of phenotypes being given by s. To consider the population dynamics, we introduce state variables $x = (x_1, x_2)$ for the densities of prey and predator respectively. The population dynamics of the two species may then be written as a pair of differential equations

$$\dot{x}_i = x_i f_i(s, x) \quad \text{for} \quad i = 1, 2 \tag{1}$$

where f_i is the per capita rate of increase of species i, and depends on s through a set of control parameters the values of which depend on the current phenotypes. These control parameters indicate how the birth and death rates caused by s influence population dynamics; for example in the familiar Lotka-Volterra equations, $\dot{x}_i = x_i\Big(r_i + \sum_j \alpha_{ij} x_j\Big)$, they are the r_i's and α_{ij}'s. The control parameters would be taken as constants in a pure ecological model, but in the presence of coevolution they may change as the phenotypic state changes, as discussed by Lewontin (1979) and Stenseth (1986). Clearly we are only concerned with systems in which the densities are bounded; moreover, the issue of coevolution only arises if the population dynamics allow coexistence of the species over a subset of S, denoted by S_c.

2.3 Population Dynamics of Resident and Mutant Phenotypes

To examine how the system evolves, we start by allowing a mutant to arise and determine what happens to its population density x_i'. Suppose a mutation occurs in species i, causing a phenotypic change δs_i in a system currently composed of individuals of phenotypes s; such a mutant is denoted $s_i' = s_i + \delta s_i$. Two factors are crucial in determining whether the mutant replaces the resident. First it should increase when rare and second it should then tend to fixation.

To determine the initial behaviour of a mutant when rare, the initial per capita rate of increase must be written in such a way that it distinguishes the phenotype of the individual under consideration from those in the environment in which it occurs. Thus we write $\widetilde{f}_i(s_i', s, x)$, where the first argument s_i' defines the phenotype of this individual, and the latter arguments s, x can be regarded as defining the biotic environment, see below. The dynamics of the system augmented by the rare mutant are therefore written

$$\begin{aligned} \dot{x}_j &= x_j \widetilde{f}_j(s_j', s, x) \quad \text{for} \quad j = 1, 2\,, \\ \dot{x}_i' &= x_i' \widetilde{f}_i(s_i', s, x)\,. \end{aligned} \tag{2}$$

The first two equations describe the dynamics of the resident phenotypes, and the last gives the dynamics of the mutant. Since the mutant is rare initially, its effect on the

biotic environment at this stage is negligible and the environment is determined by the resident phenotypes. For simplicity we assume that, before arrival of a mutant, the densities of resident populations with phenotypes s have come to equilibrium given by

$$\hat{x}_j(s): \qquad \widetilde{f}_j\big(s'_j, s, \hat{x}\big) = 0 \qquad \text{for} \qquad j = 1, 2\,; \tag{3}$$

in this case of a system at equilibrium the environment is fully specified by s, so the third argument of $\widetilde{f}_i$ is no longer needed, and we write the initial per capita rate of increase of the mutant as $\overline{f}_i(s'_i, s)$. The conditions under which the assumption of equilibrium population dynamics can be removed are considered in Dieckmann and Law (1996). A necessary condition then for the mutant to increase when rare is that it should have a positive per capita rate of increase in the environment of the resident phenotypes at their equilibrium densities, i.e.

$$\overline{f}_i\big(s'_i, s\big) > 0\,. \tag{4}$$

The eventual fate of an initially successful mutant is less easy to settle. Either it goes to fixation, thereby replacing the former resident, or both the mutant and the resident stay in the system at finite densities. For population dynamics (2) of Lotka-Volterra type (i.e. $f_i = r_i + \sum_j \alpha_{ij} x_j$), the latter outcome can typically be excluded; this is principle of mutual exclusion is proven in Dieckmann (1994). In this case, invasion implies fixation, and the phenotype of species i has made a step from s_i to s'_i. The idea here is to allow the dynamical system of population densities explicitly to drive the replacement of one mutant by another.

2.4 Phenotypic Evolution

Once a method is in place to determine whether a mutant phenotype replaces the resident phenotype, it is straightforward to consider a sequence of mutants each one replacing the phenotype that was previously present. Such a sequence, called a trait-substitution sequence by Metz et al. (1994), indicates the long-term evolutionary path of the system. The aim now is to find a system of equations describing this macroscopic evolution, in which the phenotypic traits are themselves the state variables.

As a preliminary, we make two assumptions. These are that the principle of mutual exclusion applies and that successful mutants occur rarely enough for evolution to be modelled to a good approximation by a monomorphic dynamic within species. These assumptions apply below unless otherwise stated. We caution that the assumption of monomorphism would not apply if the mutant and resident phenotypes come to persist in a protected polymorphism; Metz et al. (1994) and Dieckmann (1994) consider ways to deal with this problem.

A *selection derivative,* measuring the sensitivity of the mutant's initial rate of increase to changes in its phenotype, is central to the evolutionary dynamic. This is defined as2

$$\frac{\partial}{\partial s_i'}\overline{f}_i(s_i', s)_{s_i'=s_i} = \lim_{s_i'\to s_i} \frac{\overline{f}_i(s_i', s) - \overline{f}_i(s_i, s)}{s_i' - s_i} \tag{5}$$

where $\overline{f}_i(s_i, s) = 0$, because the resident phenotype is at equilibrium with respect to population density. Notice that the derivative is evaluated while holding the environment (defined by the equilibrium densities) constant, since it refers to a rare mutant invading at $\hat{x}(s)$. The selection derivative is important because it indicates whether phenotypic evolution takes place in the direction of greater or smaller phenotypic values; if $\partial\overline{f}_i/\partial s_i' > 0$ (respectively $\partial\overline{f}_i/\partial s_i' < 0$), then the system is vulnerable to invasions by mutants with $s_i' > s_i$ (respectively $s_i' < s_i$) with s_i' sufficiently close to s_i. One would expect, then, the macroscopic evolutionary dynamics to have a property

$$\dot{s}_i \quad \begin{cases} > 0 & \text{when} \quad \partial\overline{f}_i/\partial s_i' > 0 \\ = 0 & \text{when} \quad \partial\overline{f}_i/\partial s_i' = 0 \\ < 0 & \text{when} \quad \partial\overline{f}_i/\partial s_i' < 0 \end{cases} \quad \text{for} \quad i = 1, 2\,. \tag{6}$$

These conditions do not, of course, yet specify an evolutionary dynamic; this would entail the introduction of a scaling factor which can be dependent on the process of mutation. We will give in Section 4 such a dynamic from Dieckmann and Law (1996) that is derived from the assumption of infinitesimal mutational steps and as such applies as a close approximation for mutations of small finite size. Nonetheless, without specifying the mutation process, it is still possible to get some qualitative insights into predator-prey evolution and other kinds of coevolving systems. Notice, in particular that isoclines of zero evolution according to (6) are defined by

$$\phi_i(s): \qquad \frac{\partial}{\partial s_i'}\overline{f}_i(s_i', s)_{s_i'=s_i} = 0\,; \tag{7}$$

the fixed points in phenotypic evolution are thus given by the intersections of ϕ_1 and ϕ_2. These qualitative properties are illustrated in the next section.

3 An Example

We show how the structure above may be used in the context of a specific model investigated by Marrow et al. (1992), in which the traits s undergoing evolution are interpreted as body sizes of the prey and predator. The per capita rates of increase of phenotypes s at densities x are given by

$$\begin{aligned} \text{prey:} \quad & f_1(s, x) = r_1 - \alpha(s)x_1 - \beta(s)x_2 \\ \text{predator:} \quad & f_2(s, x) = -r_2 + \gamma(s)x_1 \end{aligned} \tag{8}$$

where r_1, r_2, α, β and γ are positive control parameters. The benefit to a predator of a prey item, $\gamma(s)$, is taken to be at its maximum for some intermediate body size

of both the predator and the prey. It is assumed that a bell-shaped function describes the relationship:

$$\gamma(s) = c_1 \exp\left(-\delta_1^2 + 2c_2\delta_1\delta_2 - \delta_2^2\right)$$

where $\delta_1 = (s_1 - c_3)/c_4$ and $\delta_2 = (s_2 - c_5)/c_6$, and c_1 to c_6 are positive parameters. On the basis that what is good for the predator is bad for the prey, the loss to the prey, $\beta(s)$, is taken to be proportional to $\gamma(s)$

$$\beta(s) = \exp\left(-\delta_1^2 + 2c_2\delta_1\delta_2 - \delta_2^2\right)$$

The term $\alpha(s)$ represents self-limitation in the prey and therefore depends only on s_1, and a quadratic function is assumed such that the prey would evolve to an intermediate body size in the absence of predation

$$\alpha(s_1) = c_7 - c_8 s_1 + c_9 s_1^2$$

where c_7 , c_8 and c_9 are positive parameters.

For certain ranges of the parameters in the functions α, β and γ, there are body sizes that permit both species to have positive equilibrium densities $\hat{x}$; the set of body sizes with this property, S_c, is delimited by the oval curve in Figure 1. As Harrison (1979) for example showed, $\hat{x}$ has global asymptotic stability given Equations (1) and (8), and this ensures that the system comes to equilibrium for a given s. Suppose that a mutation occurs causing small changes in body size to the predator or prey. A prey mutant (respectively predator mutant) increases when rare if it satisfies respectively:

$$\begin{aligned}\overline{f}_1(s_1', s) &= r_1 - \alpha(s_1')\hat{x}_1(s) - \beta(s_1', s_2)\hat{x}_2(s) > 0 \\ \overline{f}_2(s_2', s) &= -r_2 + \gamma(s_1, s_2')\hat{x}_1(s) > 0\ .\end{aligned}$$

Since these dynamics are of Lotka-Volterra type, invasion typically implies fixation. Exceptions to this principle of mutual exclusion can occur close to the isoclines $\phi_i(s)$, as discussed in Dieckmann (1994), in which case both resident and mutant may remain causing the population to become polymorphic. Usually this behaviour does not persist because evolution in the other species takes the system away from the isocline, and the system reverts to monomorphism. But it is possible for evolution to lead to a fixed point with this polymorphic property (see Section 5), in which case the monomorphic assumption underpinning the model breaks down, as discussed by Metz et al. (1994). With these caveats, conditions (6) can be used to partition Sc into regions in which evolution towards larger ($\partial\overline{f}_i/\partial s_i' > 0$), or smaller ($\partial\overline{f}_i/\partial s_i' < 0$), body size occurs for each species, separated by the isocline $\phi_i(s)$ on which there is no selection. An example is given in Figure 1, the qualitative direction of evolution being shown by the arrows.

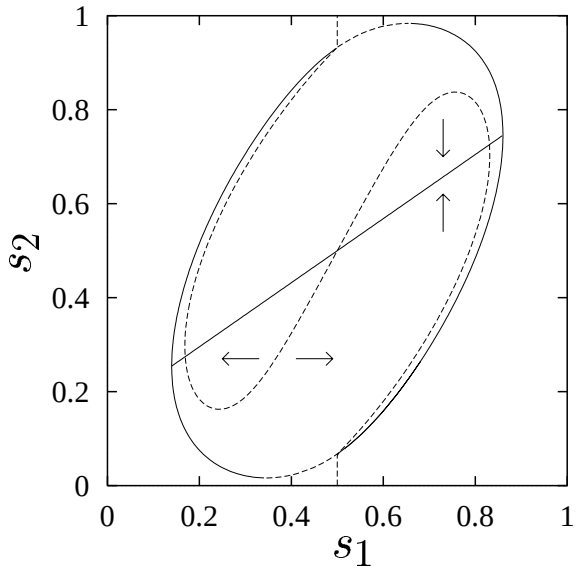

FIGURE 1 Some qualitative properties of evolutionary dynamics of prey (s_1) and predator (s_2) body size. S_c is the interior of the oval region. The line ϕ_1 is shown as discontinuous; the straight line ϕ_2 is shown as continuous. Fixed points of the system occur at the intersections of ϕ_1 and ϕ_2. Arrows indicate the direction in which body size evolves in each species, horizontal arrows for prey and vertical arrows for predators. Discontinuous part of the boundary of the oval region indicates where a prey mutant could cause predator extinction. From Marrow et al. (1992: Figure 2a), with parameters: $r_1 = 0.5$, $r_2 = -0.05$, $c_1 = 1.0$, $c_2 = 0.6$, $c_3 = 0.5$, $c_4 = 0.22$, $c_5 = 0.5$, $c_6 = 0.25$, $c_7 = 3.0$, $c_8 = 10.0$, $c_9 = 10.0$.

Simple though this approach is, it illustrates some features of a coevolving predator-prey system. First, it shows the tension typical of predator-prey coevolution. In the example given, the predator gains its greatest benefit from the prey at $s_1 = 0.5$, $s_2 = 0.5$, but the prey suffers its greatest loss here and the system does not tend to this point. Second, there is continuing evolution across the phenotype space, only terminated if the system reaches a fixed point. We should emphasize that, although evolution in this example leads to a fixed point, this is by no means an inevitable outcome, and an example is given later (Figure 2) in which the ω-limit set of the evolving system is a limit cycle — the species driving each other to continue evolving as long as the system remains in existence. Third, if one species tended to its isocline, continuing evolution would require mutations in the other species to shift it along the isocline; such evolution can be envisaged as an arms race because there would be no further change without the 'escalation' due to these mutations. Fourth, the geometry of fixed points of the system is exposed, that is, the points at which the lines ϕ_1 and ϕ_2 intersect. There can be several such points, and the properties of these fixed points are of interest in their own right (see Section 5). It can be seen that, in the case of the outer pair of fixed points, each species is evolving towards its isocline; but, in the case of the intermediate fixed point, the predator converges while the prey diverges. Fifth, the shape of S_c indicates that there is only a limited range of body sizes enabling coexistence of the species; it is

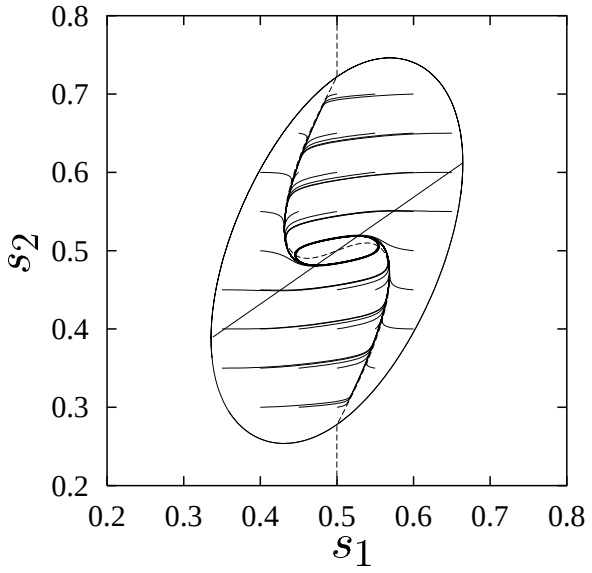

FIGURE 2 Phase portrait of a system with an evolutionary limit cycle. S_c is the interior of the oval region. The discontinuous line is ϕ_1 and the straight continuous line is ϕ_2. A fixed point of the system occurs at the intersection of ϕ_1 and ϕ_2. Curved continuous lines within S_c are orbits, all of which tend to the limit cycle around the fixed point. The dynamical system (9) is set such that $\left(\mu_1\sigma_1^2\right)/\left(\mu_2\sigma_2^2\right) = 1$; other parameters are as in Figure 1 except for $c_1 = 0.11$ (Marrow et al. 1992: Figure 2g).

possible for a sequence of mutant substitutions in the prey to lead to extinction of the predator, if they take a path across the part of the boundary shown as discontinuous. On the other hand there is no region of phenotype space in which both species have an equilibrium population density of zero, and thus there is in this example no evolutionary path in which the predator can gain such an advantage over the prey that it destroys the prey and brings about its own extinction.

4 Evolutionary Dynamics

To take the investigation of coevolution further, an explicit dynamic for the process is needed. This can be done in several ways; here we mention a stochastic trait-substitution model and one from quantitative genetics.

4.1 Stochastic Trait-Substitution Model

This models evolutionary trait-substitution sequences as directed random walks in phenotype space arising from mutation and selection. Stochasticity is induced in the evolutionary dynamics first by making the occurrence and size δs_i of mutations a random variable. Second, it comes about from the chance extinction that even advantageous mutants experience after their first appearance in a single individual, due to the effects of demographic stochasticity as discussed by Fisher (1958: 80 et seq.). These random

effects are countered by natural selection arising from the biotic environment and this imposes directionality on the random walks. A master equation for this process is derived in Dieckmann and Law (1996), and it is shown that, by taking the first jump moments of the equation (van Kampen 1981), this yields a system of ordinary differential equations

$$\langle \dot{s}_i \rangle = k_i(s) \frac{\partial}{\partial s_i'} \overline{f}_i(s_i', s)_{s_i'=s_i} \quad \text{for} \quad i = 1, 2 \,, \tag{9}$$

where

$$k_i(s) = \frac{1}{2} \mu_i \sigma_i^2 \frac{\hat{x}_i(s)}{x_u} \quad \geq 0 \,.$$

Here $\langle s_i \rangle$ is the expected phenotypic value, μ_i is the probability that a given birth is a mutant, x_u is the unit density scaling $\hat{x}_i$ to numbers, and σ_i^2 is the variance of the mutation distribution. The factor $k_i(s)$ scales the rate of evolution in species i and comprises two parts, the evolutionary rate constant $\frac{1}{2}\mu_i\sigma_i^2$ and the equilibrium population size. Notice the dependence of this system on the selection derivative (5); as a consequence the qualitative properties of the dynamics (6) remain in place, and system (9) specifies a full dynamic for the process of coevolution developed earlier. The system (9) is a first order result which is exact for mutational steps of infinitesimal size, and gives a good approximation for mutational steps of small size. The system can be refined by consideration of higher-order corrections, as derived and discussed in Dieckmann and Law (1996).

Figure 2 illustrates some evolutionary orbits of a coevolving system of predator and prey based on equations (9), having the feature that the ω-limit set is a limit cycle rather than a fixed point. This is of some biological interest because it shows that the interaction between the predator and prey is sufficient to keep the system evolving indefinitely; as discussed by Marrow et al. (1992), changes in the physical environment are not a prerequisite for continuing evolution.

4.2 Quantitative Genetics Model

In the literature, an evolutionary dynamic from quantitative genetics has most often been used. Quantitative genetics at its simplest distinguishes between two components of the phenotypic value s_i: an additive genetic part a_i and a non-genetic part e_i statistically independent of a_i. The distinction between s_i and a_i is made because selection operates on phenotypic values but only the additive genetic components are inherited, as discussed by Falconer (1989). The standard formulation of a quantitative-genetic dynamic given by Lande (1979) does not allow the per capita rate of increase (fitness) associated with phenotype s_i to depend on the environment. But Iwasa et

al. (1991), Taper and Case (1992) and Abrams et al. (1993) have suggested ways of removing this limitation. By assuming that the phenotypic distributions are narrow and that the time scale of population dynamics can be separated from that of evolution, a dynamic resembling closely that of equations (9) can be obtained:

$$\dot{\overline{s}}_i = k_i \frac{\partial}{\partial s_i'} \overline{f}_i\big(s_i', \overline{s}\big)_{s_i'=\overline{s}_i} \qquad \text{for} \qquad i = 1, 2\,, \tag{10}$$

where

$$k_i = \sigma_{a_i}^2 \qquad > 0$$

where $\overline{s}_i$ is the expected mean phenotypic value and $\sigma_{a_i}^2$ the variance of the additive genetic values, often assumed to be constant. Although not usually explicitly derived from quantitative genetics, dynamics of this kind have been used on a number of occasions; see for instance Brown and Vincent (1987a), Rosenzweig et al. (1987), Hofbauer and Sigmund (1990), Vincent (1990) and Marrow and Cannings (1993).

In view of the models' radically different starting points, the similarity of dynamics (9) and (10) is notable. They do however differ in the source of variation on which selection operates. Dynamics (10) depend on phenotypic variation due to many genes with small additive phenotypic effects placed together in different combinations; evolution is then a process of selection on these combinations as they are reshuffled through segregation and recombination. Dynamics (9) on the other hand depend on variation generated by mutation. The quantitative genetic model is well-founded empirically, whereas the mutation-driven dynamic (9) is based on a somewhat simplified notion of phenotypic variation. On the other hand dynamics (9) are derived explicitly from a stochastic process of mutation and initial increase of advantageous mutants in Dieckmann and Law (1996), and represent a natural dynamical extension to evolutionary game theory.

5 Fixed Point Properties

Much of the interest in models of coevolution has been to characterize properties of fixed points in phenotype space at which the selection pressures generated by interacting species are balanced, so that there is no further phenotypic evolution of the system. Such work has usually been developed in the context of evolutionary game theory, and a dynamic is often not made explicit in this context. Here we mention some of the literature on the application of evolutionary game theory to questions of coevolution. We then point out that the introduction of an evolutionary dynamic is necessary to determine the asymptotic stability of fixed points (in contrast to the assertions of game theory). It should be kept in mind, however, that these fixed point properties cannot tell us all we need to understand the evolutionary process for, as we have already seen, the ω-limit set of an evolutionary dynamic need not be a fixed point (Figure 2).

5.1 Evolutionarily stable strategy (ESS)

The notion of an ESS, defined by Maynard Smith and Price (1973), has been widely used to identify fixed points in phenotypic evolution, as discussed by Maynard Smith (1982). An ESS is a phenotype which, if adopted by almost all individuals in a population, cannot be invaded by a rare mutant of any other phenotype. The notion has been applied to multispecies coevolution by Brown and Vincent (1987a, 1987b) amongst others. In the context of two-species coevolution used in this paper, a sufficient condition for the phenotypes s to be an ESS is that, for individuals of phenotypes $s_i' \neq s_i$,

$$\widetilde{f}_i\big(s_i', s_i, s_j, \hat{x}(s)\big)_{s_i'=s_i} > \widetilde{f}_i\big(s_i', s_i, s_j, \hat{x}(s)\big) \qquad \begin{array}{ll} \text{for} & i,j=1,2 \\ \text{and} & j \neq i\,, \end{array}$$

recalling from (2) that the first argument of $\widetilde{f}_i$ defines the individual's phenotype, and the other arguments define its biotic environment. The set from which s_i' is drawn is discussed below. The argument s is written out in full above to distinguish the condition for an ESS from another notion given earlier by Roughgarden (1979, 1983), that of a coevolutionarily stable community (CSC); this has the property (in our notation)

$$\widetilde{f}_i\big(s_i', s_j, \hat{x}(s)\big)_{s_i'=s_i} > \widetilde{f}_i\big(s_i', s_j, \hat{x}(s)\big) \qquad \begin{array}{ll} \text{for} & i,j=1,2 \\ \text{and} & j \neq i\,, \end{array}$$

where the phenotype of the conspecific resident is not allowed to affect the per capita rate of increase of the mutant other than by the equilibrium densities, and is thus not specified. This means that the mutant's $\widetilde{f}_i$ depends on the phenotype of the conspecific resident only through the effect of the latter on the equilibrium densities. Consequently intraspecific frequency-dependent selection is excluded, and the circumstances under which the notion of a CSC applies are rather more restricted than those for the ESS, as discussed by Abrams (1989) and Taper and Case (1992). Notice that these game-theoretic properties of fixed points do not consider evolutionary dynamics, and such points may or may not be attractors in phenotypic evolution. An ESS as defined above might be better called an evolutionarily *steady* state, as this makes no reference to the dynamical notion of stability.

To add to the problems of terminology, the term ESS has also been used to refer to local asymptotic stability of equilibria of population densities in coevolutionary theory by Reed and Stenseth (1984). They envisaged a vector x of densities for resident phenotypes s, and a vector x' of densities for mutant phenotypes s', the set of phenotypes s being an ESS if the equilibrium point at which $x \neq 0$ and $x' = 0$ has local asymptotic stability for all $s' \neq s$, given that s' lies in the neighbourhood of s. This definition explicitly extends the notion of an ESS to account for population dynamics but, like the definitions above, makes no reference to evolutionary dynamics.

In these arguments and those below it is important to be clear about what set of mutant phenotypes is tested against the fixed-point phenotypes. Typically in evolutionary game theory, it is assumed that all phenotypes in S_i are tested (Maynard Smith 1982). How useful it is to test the fixed point against all possible phenotypes in coevolutionary models is debatable, because the range of phenotypes created by mutation and recombination around the current mean value is typically a small subset of S_i. As Roughgarden (1987) pointed out, one would not expect all the phenotypic variation apparent in different breeds of dogs to arise in a natural population of *Canis lupus*. To restrict phenotypic variation to a small region in the neighbourhood of the current mean is in keeping with Darwin's (1859) notion that evolution typically occurs by the accumulation of small phenotypic changes. It therefore seems more natural to use a local test, comparing the fixed point against phenotypes involving small deviations from it, as in the definition of an ESS above by Reed and Stenseth (1984); we adopt the local test below. We also restrict attention to a fixed point that lies in S_c. An interior fixed point of this kind, denoted $\hat{s}$ below, has the property that the selection derivatives $\partial \overline{f}_i / \partial s_i'$ vanish at $\hat{s}$ for both species.

5.2 Asymptotic Stability of Fixed Points

Here we review and develop some results concerning the asymptotic stability of fixed points given dynamics (9) to contrast with those from evolutionary game theory. We assume throughout that $\overline{f}_i(s_i', s)$ is continuous, twice differentiable in s_i' and s_i, and has non-zero second derivatives. The function $\overline{f}_i(s_i', s)$ then is saddle-like in s_i' and s_i around the isoclines $\phi_i(s)$; on the line $s_i' = s_i$, we have $\overline{f}_i(s_i', s) = 0$. As a preliminary, we note two properties of the isoclines. The first is *non-invasibility* such that, on $\phi_i(s)$, mutants in species i with phenotypes close to $\phi_i(s)$ are not able to invade:

$$\frac{\partial^2}{\partial s_i'^2} \overline{f}_i\big(s_i', s\big)_{s_i'=s_i} < 0 \; ; \tag{11}$$

the converse of this we refer to as *invasibility*. The notion of non-invasibility is familiar from ESS theory (Parker and Maynard Smith 1990) and the arguments of Roughgarden (1983) and Brown and Vincent (1987a, 1987b). Second is the property of *convergence* that successive mutations in species i cause evolution towards $\phi_i(s)$:

$$\frac{\partial^2}{\partial s_i'^2} \overline{f}_i\big(s_i', s\big)_{s_i'=s_i} + \frac{\partial^2}{\partial s_i \partial s_i'} \overline{f}_i\big(s_i', s\big)_{s_i'=s_i} < 0 \; ; \tag{12}$$

with the converse property of *divergence*. Attention was first drawn to the distinction between convergence and non-invasibility by Eshel and Motro (1981) and Eshel (1983), and was discussed in more detail by Taylor (1989). It is, for instance, conceivable that the isocline is non-invasible, but that starting from other points in its neighbourhood

species i evolves away from it; such a configuration has aptly been called a 'Garden of Eden' configuration by Hofbauer and Sigmund (1990).

As shown by Abrams et al. (1993), the relationship between these isoclinic properties and asymptotic stability is trivial if the dynamical system comprises only one species. If we take just one of equations (9), the Jacobian at the fixed point $\hat{s}_1$ is:

$$J = k_1(s)\left(\frac{\partial^2 \overline{f}_1(s_1', s)}{\partial s_1'^2} + \frac{\partial^2 \overline{f}_1(s_1', s)}{\partial s_1 \partial s_1'}\right)_{s_i'=s_1=\hat{s}_1}.$$

The condition for dynamical stability of a fixed point $J < 0$ thus coincides with the condition for convergence (inequality 12). Clearly, dynamical stability of the fixed point is not equivalent to non-invasibility of the fixed point.

For 2-dimensional systems as given in equations (9), the fixed points are given by the intersection of the isoclines $\phi_1(s)$ and $\phi_2(s)$, and the Jacobian at a fixed point $\hat{s}$ is

$$J = \begin{bmatrix} k_1(s)\left(\frac{\partial^2 \overline{f}_1(s_1', s)}{\partial s_1'^2} + \frac{\partial^2 \overline{f}_1(s_1', s)}{\partial s_1 \partial s_1'}\right) & k_1(s)\frac{\partial^2 \overline{f}_1(s_1', s)}{\partial s_1' \partial s_2} \\ k_2(s)\frac{\partial^2 \overline{f}_2(s_2', s)}{\partial s_2' \partial s_1} & k_2(s)\left(\frac{\partial^2 \overline{f}_2(s_2', s)}{\partial s_2'^2} + \frac{\partial^2 \overline{f}_2(s_2', s)}{\partial s_2 \partial s_2'}\right) \end{bmatrix}_{s'=s=\hat{s}}$$

As in the 1-dimensional case, the bracketed terms on the diagonal are the same as the expressions given in inequality (12), and are therefore the isoclinic conditions for convergence of each species. But there is a much more indirect relationship between these convergence conditions and dynamical stability. Abrams et al. (1993) consider the necessary and sufficient condition for local stability of a fixed point, that $\mathrm{tr}\, J < 0$ and $\det J > 0$. From this and our own work we collect together the following results for 2-dimensional systems. (i) Convergence of each species (i.e. bracketed terms in J negative) is neither necessary nor sufficient for local asymptotic stability of the fixed point. Convergence is not sufficient because, although convergence implies $\mathrm{tr}\, J < 0$, the sign of $\det J$ depends on the off-diagonal mixed partial derivatives. Convergence is not necessary because it is possible to have $\mathrm{tr}\, J < 0$ and $\det J > 0$ when one species is convergent and the other divergent. (ii) If each species is divergent, i.e. both bracketed terms of J are positive, we have $\mathrm{tr}\, J > 0$ and hence the fixed point is unstable. Thus certain classes of fixed point are definitely evolutionary repellors, but others could be either repellors or attractors. However, by allowing for conditions on the signs of the off-diagonal elements of J, three further results about these remaining fixed points can be given. (iii) If each species is convergent and the off-diagonal elements are of opposite sign, the fixed point is an evolutionary attractor. (iv) If one species is convergent, the other divergent and the off-diagonal elements have the same sign, the fixed point is an evolutionary repellor. (v) In all cases not covered by (ii), (iii) or (iv) local stability of the fixed point can be tuned just by varying the evolutionary rate constants. We conclude from these results that the simple identity of the condition for convergence

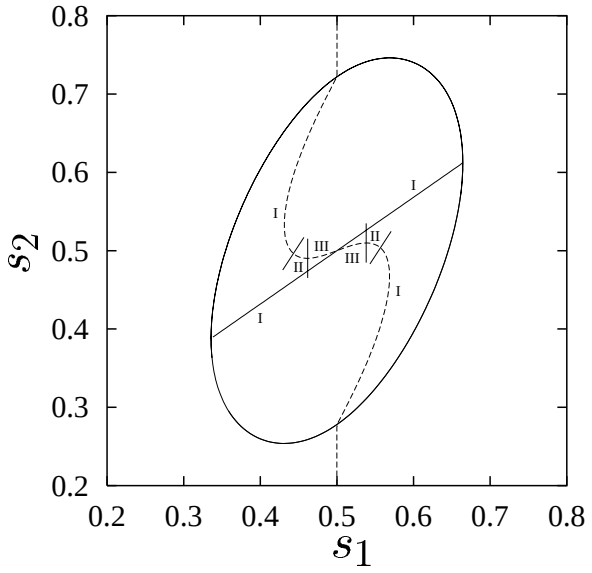

FIGURE 3 A system with isoclines such that the predator is convergent and the prey is divergent at the fixed point. S_c is the interior of the oval region. The discontinuous line is ϕ_1 and the straight continuous line is ϕ_2. A fixed point of the system occurs at the intersection of ϕ_1 and ϕ_2. The parameters defining the isoclines are as in Figure 2. Sections of the isoclines are labelled as follows. I: satisfies both inequality (11) and (12); II: satisfies (12) but not (11); III: satisfies neither (11) nor (12).

with that for local asymptotic stability, which holds for single-species evolution, has no counterpart in multispecies coevolution. In the latter case, the stability of a fixed point can depend critically on the details of the dynamical features of the coevolving system.

5.3 EXAMPLE

Figure 3 is an example which illustrates some of the results described above. At the point of intersection of the isoclines, the prey phenotype $\hat{s}_1$ has the properties of invasibility and divergence, whereas the predator phenotype $\hat{s}_2$ has the properties of non-invasibility and convergence. This example is interesting for several reasons. First, the fixed point is an example of case (v) above, i.e. its dynamical stability depends on the evolutionary rate constants. If the rate constants of the prey and predator are chosen in the ratio 1:1, the fixed point is unstable and the attractor is given by a limit cycle (Figure 2). On the other hand, if the rate constants are chosen in the ratio 1:10, allowing faster predator evolution, the fixed point becomes stable and serves as an attractor for the evolutionary dynamics (Figure 4). Second, the example illustrates how dynamical stability is independent of non-invasibility of the fixed point. It can be seen that $\hat{s}$ is an attractor in Figure 4 notwithstanding the fact that coevolution leads to a local fitness minimum for the prey. Takada and Kigami (1991) and Abrams et al. (1993) have also noted that a system of coevolving species may be driven to a fixed point where one species is at a local fitness minimum. Third, the fixed point has a

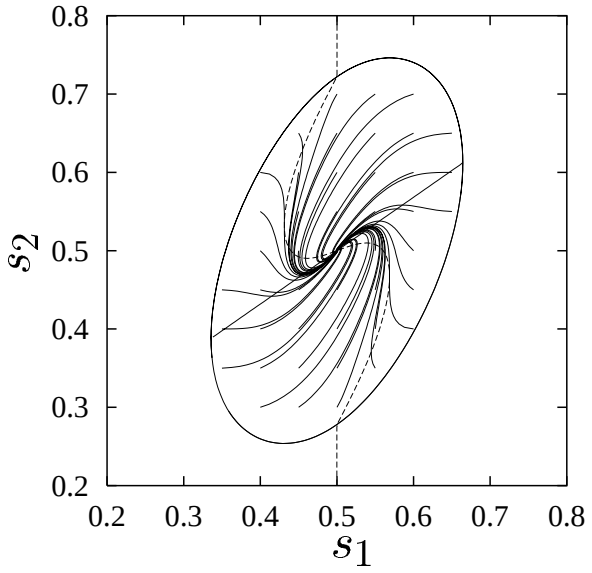

FIGURE 4 Phase portrait of a system based on the isoclines given in Figure 3. S_c is the interior of the oval region. The discontinuous line is ϕ_1 and the straight continuous line is ϕ_2. A fixed point of the system occurs at the intersection of ϕ_1 and ϕ_2. Curved continuous lines within S_c are orbits, all of which tend to the fixed point. The dynamical system is the same as that in Figure 2, except that parameters of dynamical system (9) are set to relatively slow down prey evolution: $\left(\mu_1\sigma_1^2\right)/\left(\mu_2\sigma_2^2\right) = 0.1$.

property that there is disruptive selection in the prey population and, as a result of this, two phenotypes can coexist on opposite sides of the fixed point. This can lead to evolutionary branching in the prey species, and the monomorphic evolutionary dynamic (9) ceases to be appropriate when the system reaches the fixed point, a phenomenon noted by Christiansen (1991) and discussed in depth by Metz et al. (1994). Fourth, in the system illustrated in Figure 4, the three basic kinds of selection discussed by Mather (1973: 90) are all present: selection is *directional* for both species away from the isoclines, *stabilizing* for the predator around its isocline and *disruptive* for the prey around its isocline in the neighbourhood of the fixed point.

6 Discussion

6.1 Evolutionary Game Theory and Dynamical Systems

A distinction between game theoretic methods, concerned primarily with non-invasibility of fixed points (ESSs), and more general considerations of dynamics runs rather deep through evolutionary theory. In evaluating these methods, the following points should be stressed. First, even in the evolution of a single species, non-invasibility does not guarantee dynamical stability of the fixed point. Second, in the coevolution of interacting species, neither non-invasibility nor convergence is sufficient to ensure dynamical stability of the fixed point. One needs further knowledge of the mixed

partial derivatives arising from interactions between species and on the rates at which evolutionary processes take place within species to determine whether a fixed point is an attractor. Notice in particular that the evolutionary rates and thus the evolutionary stability can depend on specific features of the mutation process, see equations (9), which therefore must not be excluded from the discussion of evolutionary phenomena.

Third and perhaps most important, there are no a priori grounds in the first place to suppose that an evolving system should tend to a fixed point; other ω-limit sets such as limit cycles or even chaotic orbits in phenotype space seem just as plausible. In fact Van Valen (1973) proposed, on the basis of palaeontological evidence, that interactions among organisms could be sufficient to cause continuing evolutionary change. As pointed out by Fisher (1958: 45), such biotic processes could be responsible for a continual deterioration in the environment experienced by a species, and Van Valen (1973) used the metaphor of the Red Queen's hypothesis 'it takes all the running you can do, to stay in the same place' from Carroll (1871) to describe the resulting evolutionary process. Such ω-limit sets are referred to as *Red Queen* dynamics in the literature by authors such as Rosenzweig et al. (1987) and Marrow et al. (1992), and an example of such a system was given in Figure 2.

Knowledge of non-invasibility and of other fixed point properties is nonetheless a helpful guide to understanding certain features of the dynamics. In particular we note that a system tending to a fixed point at which there is disruptive selection for at least one species will violate the assumption of monomorphic dynamics on which equations (9) depend. See Dieckmann and Law (1996) for suggestions as to how this problem may be overcome.

6.2 Empirical Background

To the theorist interested in entering the field of coevolution, we ought to point out that the empirical base of the subject is not strong. Although many features of living organisms are best interpreted as the outcome of a process of coevolution, rather little is known about the dynamics of the process. There is, for instance, some evidence for coevolution of predators and their prey from the fossil record of hard-bodied organisms; see for example Vermeij and Covitch (1978), Kitchell et al. (1981), Vermeij (1982,1983, 1987), Bakker (1983), Stanley et al. (1983), West et al. (1991). But in such examples one sees only an outcome of the evolutionary dynamics, and the dynamics themselves are not readily reconstructed. A rare exception in the case of host-pathogen evolution is myxomatosis in Australia documented by Fenner and Ratcliffe (1965) where, following the release of the myxoma virus in 1950, the virulence of the myxoma virus declined as did the susceptibility of the rabbit; from the information available, some inferences about the evolution of virulence can be made from the data, as discussed by Anderson

and May (1982) and Dwyer et al. (1990). There is unfortunately no experimental basis in coevolution to match, for instance, the experiments of single-species quantitative genetics where selection differentials can be applied to specific traits and responses to selection measured, as described by Falconer (1989). This is not altogether surprising, because the experimental problems of getting two or more interacting species to live together while each generates selection differentials on the other(s) are, to say the least, substantial. Yet experiments along these lines are needed to set the evolutionary dynamics of coevolution on a firm empirical base and to guide development of theory.

We end with three suggestions about possible directions for future research.

6.3 Community Coevolution

We have considered a simple case of coevolution involving two species, it being straightforward in this case to visualise the geometry of evolutionary dynamics. In reality matters are more complicated since it is rare for a predator and prey species to live in isolation of other interactions; as reviewed by Pimm et al. (1991), typically they would be embedded in a food web with other species. Unless the interactions between a particular pair of species are much stronger than those with others, one needs to think of the traits evolving as a result of an ensemble of the selection pressures of all the species present, a process referred to as diffuse coevolution by Janzen (1980). The issue of how these larger communities evolve is of interest in its own right, and there is much to be done to develop a mathematical framework for such investigations. Some steps in this direction are the lag-load model of Maynard Smith (1976) and Stenseth and Maynard Smith (1984), the plant-herbivore model of Levin et al. (1990), the rugged fitness landscape models of Kauffman and Johnsen (1991) and Kauffman (1993), and the predator-prey community model of Brown and Vincent (1992).

6.4 Evolution of Population Dynamics

As phenotypic evolution takes place, the control parameters of population dynamics will typically change and this may lead to qualitative changes in the population dynamics, for instance a change from an equilibrium to a non-equilibrium ω-limit set for population densities. There have been few attempts to document this experimentally, although Stokes et al. (1988) have suggested that changes observed in the population dynamics of a laboratory population of blowflies were consistent with evolution from oscillatory to equilibrium population dynamics. Data from natural populations such as those collated by Hassell et al. (1976) have suggested that chaotic dynamics are rather rare; on the other hand recent research by Rand and Wilson (1991) and Turchin and Taylor (1992) suggests that such dynamics do occur. A question that arises from the feedback from evolution to population dyanamics is whether there could be a tendency for equilibrium

attractors for population density to come to prevail in natural systems. Work by Hansen (1992), Metz et al. (1992), Gatto (1993) and Godfray et al. (1993) argues for this. But whether there is a general mechanism (based on individual selection) for evolution to do so is open to debate, and needs further investigation.

6.5 Adaptive Landscapes

One might ask if some property of the species increases during their coevolution, that is, whether in some sense the species are 'improving' on an absolute scale. The metaphor of an adaptive topography, which envisages that phenotypic values of a species can be mapped on to a scale of mean population fitness to produce a hilly landscape, has been widely used in evolutionary theory. Evolution is then seen as a process of hill climbing until a local maximum in mean fitness is reached. But it is not at all clear that this metaphor is appropriate if selection is generated by interactions within the system as opposed to factors set externally (e.g. abiotic factors such as temperature and humidity). Let us consider two interpretations of this metaphor. We will examine evolution in one of the species, and assume that the system is at some point s in a phenotype space prior to a mutation in this species, with population dynamics that have settled to equilibrium. Suppose an advantageous mutant starts to spread. (i) A first obvious interpretation of mean fitness would be the population's mean per capita rate of increase. But this measure is not appropriate because the total population density may decline as the mutant starts to spread; from a starting height of zero, the mean per capita rate of increase would then become negative and the path of evolution would be down a surface defined by this measure. (ii) An alternative interpretation would be to use a surface defined by the initial per capita rate of increase of mutants in the environment s, the slope of which is given locally by the selection derivative (5) indicating the correct direction of evolution. Yet, by the time the mutant reaches fixation, it has a per capita rate of increase of zero. Thus, based on this second measure, there is no overall gain arising from the evolution, and we conclude that it remains debatable as to how appropriate a hill-climbing metaphor is in the context of coevolution. This leads us to ask what, if any, metaphor would be appropriate to describe a process of coevolution, and under what circumstances there exists a function that is maximized during the course of evolution.

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