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Dynamics and Evolution: Evolutionarily Stable Attractors, Invasion Exponents and Phenotype Dynamics

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Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics

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SUMMARY

We extend the ideas of evolutionary dynamics and stability to a very broad class of biological and other dynamical systems. We simultaneously develop the general mathematical theory and a discussion of some illustrative examples. After developing an appropriate formulation for the dynamics, we define the notion of an evolutionary stable attractor (ESA) and give some samples of ESAS with simple and complex dynamics. We discuss the relationship between our theory and that for ESSS in classical linear evolutionary game theory by considering some dynamical extensions. We then introduce and develop our main mathematical tool, the invasion exponent. This allows analytical and numerical analysis of relatively complex situations, such as the coevolution of multiple species with chaotic population dynamics. Using this, we introduce the notion of differential selective pressure which for generic systems is nonlinear and characterizes internal ESAS. We use this to analytically determine the ESAS in our previous examples. Then we introduce the phenotype dynamics which describe how a population with a distribution of phenotypes changes in time with or without mutations. We discuss the relation between the asymptotic states of this and the ESA. Finally, we use our mathematical formulation to analyse a non-reproductive form of evolution in which various learning rules compete and evolve. We give a very tentative economic application which has interesting ESAS and phenotype dynamics.

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1. INTRODUCTION

We present a dynamical theory of Darwinian evolution in ecosystems. In doing this we address the problems associated with coevolution and dynamics. Our theory deals with complex dynamics such as the oscillations and chaos found in many model ecosystems. It is coevolutionary in the sense that the evolutionary environment of a given species is the interacting ecology of coexisting species. The evolution of this species must be seen in the context of the coevolution of the complete local ecological structure.

We start by extending the ideas of evolutionary dynamics and stability to a very broad class of biological and other dynamical systems. Firstly, we show how to formulate biological dynamics so that the notion of evolutionary stability of general attractors can be defined. Such evolutionarily stable attractors (ESAs) are stable to small invasions by populations with mutant phenotypes or behaviour. They generalize Maynard Smith's evolutionarily stable strategies. A phenotype p for which there is an ESA is called an *ESA value*. The dynamics of both pure and mutated systems are determined by the pure equations and interaction functions of the given system. If the dynamics are the mixed strategy population dynamics of linear evolutionary game theory, then we recover the condition for an ESS due to Maynard Smith and Price (Hines 1987; Maynard Smith & Price 1973; Maynard Smith 1982; Zeeman 1979, 1981). However, our approach both allows a unified treatment of the various cases within this classical theory (such as playing the field and asymmetric competition) and also deals with a much wider range of nonlinear and dynamical situations. We illustrate this first by considering constrained coevolution of a resource–predator–prey system and also a modification of the classical Hawk–Dove game (Maynard Smith 1982). In the latter example, the individuals are predators and the resource being competed for is a share of the prey population that is changing dynamically. The first of these two systems has a chaotic ESA for some parameter values. For others, it has multiple ESAs separated by evolutionary repellors. In such a case the path of evolution is not uniquely determined†.

The Hawk–Dove predator–prey example has two dynamical ESAs. One of them corresponds to that found in the classical theory (after taking time-averaged values for the resource). The other is a boundary ESA where only Hawk-like behaviour is observed. Its existence is a consequence of the inclusion of the dynamical prey. Moreover, these ESAs can be quasiperiodic.

In § 4 we then introduce the the *invasion exponent* $\vartheta_p(p') = \vartheta_p(\Lambda, p')$ which characterises the evolutionary stability of an attractor Λ, corresponding to a phenotype p, to small mutant populations with phenotype p'. It measures the rate of growth of the invading population. This is our main mathematical tool for the analysis of ESAs. Using it we are able to check the evolutionary stability or instability of quite complicated systems with interesting dynamics. The correct mathematical definition of ϑ is non-trivial and important to get right, and is given in § 4. We also derive analytic expressions for ϑ in a number of interesting situations. For example, it is easily calculated for stationary, periodic and quasiperiodic attractors. For Lotka-Volterra systems it is determined at the fixed points of the system even if the attractor is chaotic. We give a numerical algorithm for calculating ϑ when this cannot be done analytically. Section 4 is the most mathematically sophisticated part of the paper because, for chaotic attractors, it requires the use of ideas from ergodic theory and many of the results have to be couched in terms of invariant measures.

We also use the invasion exponent to define a new function $s(p) = (s_1(p), \ldots, s_s(p))$ which we call the *differential selective pressure.* It measures certain gradients of the invasion exponent as the phenotype is varied through p. If p is interior to the phenotype constraint manifold P, then a sufficient condition for p to be an ESA value is that $s(p) = 0$ and that various partial derivatives $d_{p_i} s_i(p)$ are negative (or negative definite in the case of multi-dimensional p). This is the generic situation for nonlinear systems and brings to light a degeneracy of the linear games. For these, if p is an ESS value, then the derivative of s is identically zero. This is why the usual ESS condition of Maynard Smith and Price (given in equation (2.4) of Maynard Smith (1982)) contains a condition which is second-order. Generic nonlinear systems only need first-order conditions. For these, if $p = p_*$ is an ESA value, the function $\vartheta_p(p')$ is nonlinear. It has a quadratic maximum at p and takes value 0 there.

In § 5 we introduce phenotype dynamics. These are also completely determined by the pure equations and interaction functions of the system together with a mutation process. They describe the dynamics of phenotypic distributions. A distribution of phenotypes is present in the population and we study the way in which it changes through time. We show that in some cases the phenotype dynamics agree with the ESAs and the system converges to a distribution which is close to a delta function based at the ESA phenotype. (Of course, the amplitude varies dynamically.) However, in others, the asymptotic distribution is more complex. For example, in some cases, it has much greater phenotypic variation and, in others, the competition between multiple ESAs leads to very interesting phenotype dynamics. The simple case is observed in our resource–predator–prey model. The only complication is that when there are two ESAs, then for widely spread initial conditions, one of these dominates the other.

The Hawk–Dove predator–prey system is different. As mentioned above for mixed strategies, there were two ESAs: an interior one corresponding to that observed in the classical game and a boundary ESA where only Hawk-like behaviour is observed. If all the initial strategies are close to this boundary situation, then the asymptotic distribution is close to a delta function at the boundary. On the other

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† In a future paper (Rand & Wilson 1993) we discuss the relationship between the bifurcations of such multiple ESAs and punctuated equilibria.

hand, all other initial distributions converge to a non-trivial widely spread distribution. This is supported on the whole phenotype space and has its mean at the interior ESA. Thus, although it has the expected mean, the asymptotic state has great phenotypic variation. In § 5*d*(i) we show that this is a consequence of the above-mentioned degeneracy of the linear games.

If instead of mixed strategies we consider polymorphic populations, where each individual is forced to play a pure strategy, then our phenotype dynamics are analogous to those introduced by Taylor & Jonker (1987). However, the behaviour is much richer. We observe complicated oscillatory irregular behaviour rather than the usual equilibrium. This example demonstrates that mixed strategy dynamics can differ greatly from polymorphic population dynamics even within the same system.

We also consider a predator–prey system in which the prey adopts a strategy p which weights the relative importance given to searching for food or avoiding predation. This has multiple ESAs and this multiplicity is reflected in the phenotype dynamics. Initial distributions converge to a state where they oscillate in an irregular way between two opposing distributions. One consists mainly of risk-averters while the other mainly consists of risk-takers. It is tempting to think of this as a biological business cycle.

Finally, in the last section we consider a possible non-reproductive application of these general ideas. The general situation we have in mind is a system in which agents adopt strategies in the face of both a dynamical environment and their appreciation of the actions of other agents. The dynamic which determines the changes in the agents strategies corresponds to some sort of learning. We are interested in both the dynamics of such a situation and the evolution of the learning process. It is this learning process which is regarded as the phenotype p. In this context we are only able to present a very modest example. We model learning using discounted payoffs and use an economical version of our Hawk–Dove predator–prey system. In this we think of the prey as consumers and the predators as producers that adopt either costly high-risk aggressive methods of selling or low-risk passive ones. We then investigate the evolution of the residual preferences of the learning process.

We introduce the various mathematical ideas by the series of examples described above. These are not necessarily meant to be biologically realistic, but rather to indicate the richness of our approach and to convince the reader that it can usefully be applied to realistic situations. In particular, in each of the cases we consider, the dynamics will be given by a mapping. Thus, time is discrete. The biological justification for this usually involves the non-overlapping nature of generations. In our case it is simply mathematical and expository convenience. All the ideas we discuss extend without difficulty to continuous time and ordinary differential equations. In addition, we believe that they apply to a much wider class of systems including stochastic processes and spatially extended systems such as partial differential equations, coupled map lattices and cellular automata. We indicate the changes that are necessary for ordinary differential equations in Appendix 1.

At this point we would like to say a few words about our interpretation of coevolution which in some aspects looks ahead to some of our results. The simplest form of evolution occurs when only the phenotype p_j of a single species j changes. Nevertheless, the evolutionary stability of that change is determined by the whole local ecological dynamics. Coevolution is where the ecology's phenotype vector p changes with respect to more than one species. Let $p'_1, \ldots p'_s$ be the new species phenotypes. For this coevolution, we require that at least two of the phenotypes p'_i have changed. Let $y = (y_{i_1}, \ldots, y_{i_k})$ be an invading population of several species with these new phenotypes p'. Then the pure system with phenotype p is unstable to invasion by y if, and only if, it is unstable to invasion by at least one of the single-species populations given by y_{i_j}. Thus, a complex population can invade if, and only if, one of the simple ones that make it up can. This fact is the content of proposition 4 of § 4*b*.

In related work Cressman (1990) has considered evolutionary stability in ecological systems at an equilibrium point and Marrow *et al.* (1992) have carried out an extensive analysis of selective pressures in a Lotka–Volterra predator–prey system. The latter work considered the relation between ESSs and Red Queen evolution. This question was also addressed by Rosenweig *et al.* (1987). In this paper the problem of evolutionary stability and instability for equilibrium ecologies is also formulated and a dynamic on phenotype space defined by selective pressure is introduced. An alternative approach to evolutionary stability in density-dependent systems is contained in Brown & Vincent (1987). However, this follows a different and more limited approach than ours and depends upon the existence of a so-called fitness generating function. In a short survey article Metz *et al.* (1992) address some related topics. In particular, paralleling our invasion exponent, they consider the use of Lyapunov exponents to characterize fitness and study invasions.

Parts of the paper are very mathematical and use concepts that, although they are necessary to our development, are not in common use outside of mathematics. This is particularly true of § 4. We therefore recommend that, on a first reading, the biological reader should omit all of this section but its introduction.

2. PRELIMINARY MATHEMATICAL FRAMEWORK

(*a*) *Mathematical framework and an example*

We start by considering a simple example with the aim of illuminating the general mathematical discussion that follows.

Table 1. *An explanation of the construction of equation (1)*

term in equation	interpretation
$1+b_1$	prey's unconstrained birth rate
$-\alpha\frac{x_1}{x_3}$	decrease in fitness of prey due to resource limitation
$-c_1\frac{x_2}{1+d_1x_1}$	decrease in fitness of prey due to predation
$1-d_2$	predator's unconstrained death rate
c_2x_1	predator's fitness increase due to feeding
$1+b_3$	resource's unconstrained reproductive rate
$-\frac{x_3}{k}$	resource's carrying capacity limitation
$-c_3x_1$	resource's fitness decrease due to feeding by prey

The example is a resource–predator–prey system with the following dynamics

$$\frac{x_1'}{x_1} = (1+b_1)\exp\left(-\alpha\frac{x_1}{x_3} - c_1\frac{x_2}{1+d_1x_1}\right),$$

$$\frac{x_2'}{x_2} = (1-d_2)\exp(c_2x_1),$$

$$\frac{x_3'}{x_3} = (1+b_3)\exp\left(-\frac{x_3}{k} - c_3x_1\right). \qquad (1)$$

Here x_1, x_2 and x_3 denote respectively the population size of prey, predators and resource and the primed variables represent the corresponding numbers in the next period. The biological interpretation of the various terms in the equation is outlined in table 1. We do not attempt to defend this model on grounds of realism. It is just used here as an illustrative example. As the parameters are changed, it displays a wide range of dynamical behaviour including periodic, quasi-periodic and chaotic attractors. For example, it is chaotic when the parameters are as in table 2. The attractor for the first set of these parameter values is shown in figure 1.

In this example we distinguish three groups of species: resource, predator and prey. In the pure system there is one species in each group. However, we want to consider the effect of adding mutant resources, predators and prey. Therefore, we will allow for mutations within each group and thus consider systems with more than one species in each group.

We can write equation (1) in the abstract form

$$x_i' = X_i(x,p) \qquad (i=1,\ldots,s), \qquad (2)$$

showing the dependence of the dynamics upon the phenotype parameter. In our example $s=3$.

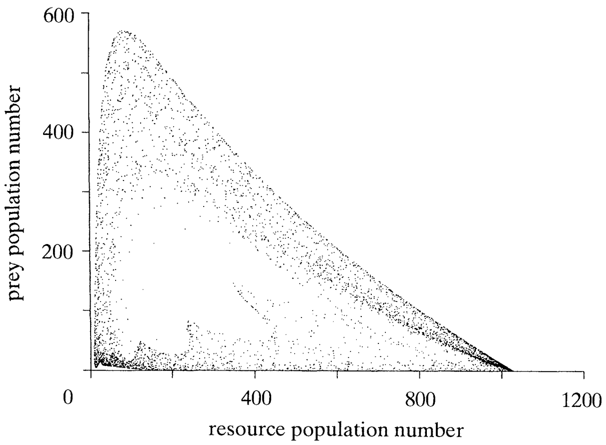

Figure 1. A two-dimensional projection of the attractor for equation (1) with the first set of parameters as in table 2.

(i) *Phenotypes*

At this point it is important to discuss the relation between phenotype and dynamics. We regard the phenotype of a species group i as being described by a vector p_i of real numbers. Thus each aspect of the phenotype is capable of continuous variation. We let P_i denote the set of possible values that p_i can take. By p we denote the vector $(p_1,\ldots,p_s)$ which encodes all the phenotypes of our pure system. One can think of p as representing the ecosystem's phenotype. The set of values which p can take is denoted by P.

The dynamics and evolution of a system such as that described by equation (1) is determined by the parameters that occur in the equations. Each of these parameters is a function of some subset of the p_i. In the resource–predator–prey model, equation (1) involves the parameters $\alpha=\alpha(p_1)$, $b_i=b_i(p_i)$, $d_i=d_i(p_i)$ and $k=k(p_3)$, as well as the parameters c_1, c_2 and c_3 which depend upon the phenotype of more than one species group. Because the parameters are functions of the phenotypes they are not independent and there may be constraints on the values that they can take.

If the phenotypes p_i are allowed to vary independently, then P is the Cartesian product of the sets P_i. However, within our framework, it is often legitimate and useful to replace the phenotypes by a subset of the parameters that occur in our dynamical equations. Hence we ignore aspects of the phenotypes that do not affect the parameters and so we can regard the parameters as the phenotype itself. This is permissible because the phenotypes only express themselves through these parameters.

These parameters are often constrained. For example, it may not be possible to increase one without decreasing another. When we regard the parameters as defining the phenotypes, then the phenotypic constraint manifold P is the set of all possible values of

Table 2. *Parameter values for equation (1). These give chaotic dynamics*

α	b_1	b_3	c_1	c_2	c_3	d_1	d_2	k
0.3	1.1	1.8	0.0025	0.0015	0.005	0.01	0.05	1000
0.5	1.1	2.8	0.001	0.0005	0.005	0.01	0.05	1000

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the vector of parameters. Because of the constraints the dimension of this is often less than the number of parameters. In this case P is a proper subset of the Cartesian product of the P_i.

These constraints on p are represented by the structure of P and this is why we call P the *phenotypic constraint manifold*.

Later in this section we discuss the advantages gained by using the parameters as phenotype. The main advantage is the removal of phenotypic redundancy.

There are two sorts of constraints. The first concerns constraints internal to P_i. For example, these may occur because two parameters in the equation for the ith species group $a = a(\pi)$ and $b = b(\pi)$ are functions of a single component π of p_i. Then locally b will be a function of a. Also, there are often constraints imposed by energy and resource limitations[‡]. We will see that the existence of these internal constraints is very important for the existence of ESAS[§] and is also an important natural property of real ecosystems.

The other constraints are cross-group constraints where a parameter in the equation for the ith species group depends upon some of the phenotypes p_j with $j \neq i$. This is the case, for example, for the parameter c_1 in equation (1) which depends upon the phenotype of both the prey and the predator. However, it is usually the case that these parameters are part of the interaction terms that we are going to define below. It then follows that their dependence upon the p_j for which $j \neq i$ is not relevant to the question of evolutionary stability. This is explained in detail in remark 1 of § 4*c*. We continue the discussion of these cross-terms after introducing the interactions.

Our approach allows for the simultaneous coevolution of all the species phenotypes, and all our general ideas are developed in this context. However, in the examples that we treat, we often constrain the phenotype and only consider mutations of a single phenotypic attribute or of several that are linked together and determined by a single parameter.

(ii) *Interactions*

Let us now return to our example and suppose that a mutant prey species is present, consisting of y_1 individuals. Then to the equation (1) we must add an equation for y_1 similar to that for x_1 but with a different value p_1' of the phenotypic parameter p_1. The original and mutant prey will compete for the same available resource x_3. The resource-limiting term in equation (1) is $\exp(-\alpha x_1/x_3)$ which expresses the effect of the magnitude of the number of prey per unit of resource. When the mutant population y_1 is present, the number of prey per unit of resource is instead $(x_1 + y_1)/x_3$. Thus, the resource-limiting term should be replaced by $\exp(-\alpha(x_1 + y_1)/x_3$. In fact, in general it should be of the form $\exp(-e_{11}/e_{13})$, where e_{1i} is the total number of individuals belonging to a species in group i.

It is necessary for our development to single out such terms e_{ij} which represent those quantities of species group j which enter the equations for group i. We call them interaction terms and incorporate them in our formulation. Thus, we rewrite equation (1) for the pure dynamics as

$$\frac{x_1'}{x_1} = (1 + b_1)\exp\left(-\alpha\frac{e_{11}}{e_{13}} - \frac{e_{12}}{1 + d_1 e_{11}}\right),$$

$$\frac{x_2'}{x_2} = (1 - d_2)\exp(e_{21}),$$

$$\frac{x_3'}{x_3} = (1 + b_3)\exp\left(-\frac{e_{33}}{k} - e_{31}\right), \tag{3}$$

where e_{11} is the population sized of the prey ($= x_1$ in this pure case), $e_{13} = e_{33}$ is the population size of the resource ($= x_3$ in this pure case), and the other e_{ij} are the jth species group population weighted mean of $c_i = c_i(p_i, p_j)$.

Before proceeding let us further clarify the nature of the interaction parameters $e = (e_{ij})$. In general e_{ij} is a function of the phenotypic distribution ξ_j of the jth species group and the phenotype p_i. Thus we write $e_{ij} = e_{ij}(\xi_j; p_i)$. Such a distribution $\xi_j = x_j\, dp_j$ records the phenotypic density of the species group j population, i.e. the number of individuals in species group j whose phenotype lies in the volume dp_j based at p_j. For each p_i, $e_{ij}(\xi_j; p_i)$ is either a number or a vector.

For example, in our resource–predator–prey example above (equation (3)), we take[‖]

$$e_{11}(\xi_1; p_1) = \text{prey population size} = \int \xi_1(\pi_1)\mathrm{d}\pi_1,$$

$$e_{21}(\xi_1; p_2) = \text{prey population weighted mean of } c_2,$$

$$= \int c_2(p_2, \pi_1)\xi_1(\pi_1)\mathrm{d}\pi_1. \tag{4}$$

Note the dependence of the various $e_{ij}(\xi_j; p_i)$ upon p_i. In particular, e_{11} is independent of p_1 in this example while e_{21} does depend upon p_2.

If $\xi = (\xi_1, \ldots, \xi_s)$ gives the phenotypic density of all species groups, by $e(\xi; p)$ we denote the matrix $(e_{ij}(\xi_j; p_i))_{i,j=1,\ldots,s}$ (which may have vector entries) and by $e_i(\xi; p)$ we denote $(e_{ij}(\xi_j; p_i))_{j=1,\ldots,s}$.

(iii) *The pure dynamics*

In the pure case the distribution ξ_j is $x_j \delta_{p_j}$ where δ_{p_j} is the delta function on P_j concentrated at p_j. There is

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[‡] In some cases the constraints are of the form $f_j \leqslant C_j$ where f_j is a function of the phenotypes present in the system. In such a case, the interesting evolutionary stable phenotypes are usually on the boundary ∂C of the constraint set C. The boundary ∂C is given by $f_j = C_j$. It may then be desirable to take $P = \partial C$. In particular, this may reduce the dimension of the permitted phenotypic variations without altering any conclusions.

[§] This is relevant to the debate on the Red Queen Hypothesis. We would suggest that this hypothesis is essentially equivalent to the non-existence of ESAS. Therefore, in view of our results, its veracity is largely equivalent to the absence of constraints that enhance the possibility of an ESA. The debate should therefore concentrate upon understanding the structure of these constraints in real ecosystems. We discuss the question in more detail in Rand & Wilson (1993) and Rand (1993). Also see Rosenweig *et al.* (1987) and Marrow *et al.* (1992).

[‖] We will use π_j to denote the phenotype of the jth species group when we are thinking of this as a variable to be integrated over. This leaves the symbols p_j and p_j' free to stand for the specific phenotypes of the pure and mutated systems.

only one phenotype present. Thus the distribution of all species groups is given by the vector $(x_1\delta_{p_1}, \ldots, x_s\delta_{p_s})$ which we denote by $x\delta_p$. Then the overall interaction $e(x\delta_p;p)$ for the pure case is given by the matrix $(e_{ij}(x_j\delta_{p_j};p_i))$. Thus we write our pure equations such as (3) in the abstract form as

$$x_i' = X_i(x,e_i,p) \qquad (i = 1, \ldots, s),$$

$$e_i = (e_{ij}(x_j\delta_{p_j};p_i))_{j=1,\ldots,s}. \tag{5}$$

We call this the pure dynamics of the system.

This formulation has been derived in detail because all our definitions and constructions follow from the form of the pure equations and the interactions. Note that, in the pure case, with the interactions given by equation (4),

$$e_{21} = e_{21}(x_1\delta_{p_1};p_2) = \int c_2(p_2,\pi_1)x_1\delta_{p_1}\,\mathrm{d}\pi_1$$

$$= c_2(p_2,p_1)x_1 = c_2x_1,$$

as is desired.

Now we consider how to introduce a small mutant population $y = (y_1, \ldots, y_s)$ with phenotype $p' = (p_1', \ldots, p_s')$. The new phenotypic distribution is given by

$$x\delta_p + y\delta_{p'} = (x_1\delta_{p_1} + y_1\delta_{p_1'}, \ldots, x_s\delta_{p_s} + y_s\delta_{p_s'}),$$

and therefore the equations for the new system are given by

$$x_i' = X_i(x,e_i,p) \qquad (i = 1, \ldots, s),$$

$$y_j' = X_j'(y,e_j',p') \qquad (j \in M),$$

$$e_i = (e_{ij}(x_j\delta_{p_j} + y_j\delta_{p_j'};p_i))_{j=1,\ldots,s},$$

$$e_i' = (e_{ij}(x_j\delta_{p_j} + y_j\delta_{p_j'};p_i'))_{j=1,\ldots,s}, \tag{6}$$

where M is the set of i such that $p_i' \neq p_i$. We express the equation in this way because we do not want to include equations for mutants which do not differ from the original species.

We call this system the *p'-mutated equation* and note that it is completely determined by the pure equations and the interactions.

When the interactions are given by equation (4) then

$$e_{21}(x_1\delta_{p_1} + y_1\delta_{p_1'};p_2) = \int c_2(p_2,\pi_1)(x_1\delta_{p_1} + y_1\delta_{p_1'})\mathrm{d}\pi_1,$$

$$= c_2(p_2,p_1)x_1 + c_2(p_2,p_1')y_1.$$

This motivates an extra natural condition that we will impose on our interactions for mathematical convenience. Suppose that we have a population in species group j with a finite number of phenotypes $p_j^1, \ldots, p_j^k$ present. Then we denote $e_{ij}(x_1^1\delta_{p_j^1} + \ldots + x_1^k\delta_{p_j^k};p_i)$ by $e_{ij}(x_1^1, \ldots, x_1^k;p_i)$ or $e_{ij}(x_1^1, \ldots, x_1^k,p_1^1, \ldots, p_1^k;p_i)$ and demand that e_{ij} is a smooth function¶ of $(x_1^1, \ldots, x_1^k)$, $(p_1^1, \ldots, p_1^k)$ and p_i. This is the case for all the examples discussed here. We also note that, with these definitions, $e_{ij}(x,0;p_i) = e_{ij}(x;p_i)$. Consequently,

$$e_{ij}(x_j,y_j;p_i) = e_{ij}(x_j;p_i) + y_j\,e_{ij}^1(x_j,y_j;p_i), \tag{7}$$

for some smooth function $e_{ij}^1(x_j,y_j;p_i)$.

Although in the above example e_{ij} is a scalar, in general it can be a vector quantity. This is the case for example for the system with strategic prey in § 5*c*. In general, the species groups may interact through different average properties such as abundance, density, mean strategy, average clustering, biomass, etc.

In the general case, the variable x_i is any suitable parameterisation of the population of group i and may involve age or size structure. Thus x_i and y_i may be multi-dimensional vector quantities.

We now continue our discussion of phenotypes and cross-equation constraints. As we have seen, the interaction e_{ij} contains these cross-equation parameters which are in the equation for species group i but depend on the phenotype of a different group j. This interaction will either be a constant or depend upon p_i alone. Throughout the paper, we will denote by q_i the vector of all those parameters and interactions which depend upon p_i. Our above-stated intention of often identifying phenotype with parameters will usually be implemented by taking $q = (q_1, \ldots, q_s)$ for the phenotype vector p of the ecology when this is appropriate.

We can now comment further on the redundancy of too high dimensional phenotypes discussed above. Suppose that some character π of the phenotype has no influence upon the parameters of the equation. Then the behaviour of the system is independent of π. Thus, we can get evolutionary drift with respect to π and the system cannot be evolutionarily stable for this trivial reason. A similar remark holds if the dimension of p is greater than the number of parameters. Then we expect subsets of positive dimension in P to give rise to the same parameter values. Evolutionary drift can occur along these. These trivial obstructions to evolutionary stability should be removed by restricting p to only those characters that play a definite role in setting the parameters. One way to do this is to use the parameters and interactions to define the phenotype. Usually, one can take q to be the ecology's phenotype vector p. In this case, there is an exact balance in the equation $s(p) = 0$ for evolutionary stability (see § 4*c*). Thus, generically, we will obtain isolated points p as solutions and hence as ESA values. This is explained further in § 4*c*(i).

(*b*) *Evolutionarily stable attractors*

Now we suppose that equation (5) has an attractor Λ. It is well-known that the equations of population dynamics have a rich variety of attractors including stationary, periodic, quasi-periodic and chaotic ones. One advantage of our approach is that it applies to all these cases.

We now make the standing assumption that if a species has a zero population then equation (5) implies that it remains zero for all time. The only way it can become non-zero is by mutation. Then the set

$$\Lambda_0 = \{(x,y) : x \in \Lambda, y = 0\},$$

is an invariant set for the dynamics of the p'-mutated equation (6).

Definition 1. The attractor Λ of the pure system (5) is said

¶ A C^r function is one that is r-times differentiable and has continuous derivatives. For the purposes of this paper by a smooth function we mean one that is C^3.

to be *strongly evolutionarily stable* if for all p' in P near p, Λ_0 is an attractor for the p'-mutated system (6).

This means that for all p' in P near p, a small invading mutant population y will die out and the system will relax back to its pure state. For deep mathematical reasons (see Appendix 2), this turns out to be too strong a condition for chaotic attractors because generically there are always ways in which chaotic attractors can be invaded. However, the possible invasions have measure zero in some sense and are therefore not observed and irrelevant. Therefore, we use the slightly weaker definition of evolutionary stability given below. For non-chaotic attractors the strong evolutionary stability and the weaker form are equivalent. Experience shows that for practical purposes this is as effective a condition as strong evolutionary stability. Moreover, we conjecture that, in systems with a small amount of stochastic noise, the two notions are equivalent. This conjecture is based on numerical experiments and some preliminary mathematical research.

The weaker notion of evolutionary stability means that the probability of very small invasions succeeding is very small and goes to zero with the size of the invasion. It is precisely defined as follows. Let U be a neighbourhood of Λ in the x-space. Let U^ε denote the set of all points (x,y) such that $x \in U$ and $\|y\| < \varepsilon$. Let $\Lambda^\varepsilon_{p'}$ denote the set of all points $(x,y) \in U^\varepsilon$ such that, if $(x_n, y_n) = g^n(x,y)$, $\|y_n\| \to 0$ as $n \to \infty$.

Definition 2. We say that Λ is *evolutionarily stable* to p' if the Lebesgue measure of the set of points in U^ε but not in $\Lambda^\varepsilon_{p'}$ tends to 0 as $\varepsilon \to 0$. We say that Λ is *evolutionarily stable* if it is evolutionarily stable to p' for all p' in P near p.

We call such an attractor an ESA. The associated phenotype p is called an ESA value. We say that Λ is *globally evolutionarily stable* if this stability holds not only for small perturbations p' of p in P, but also for all p' in P.

The precise form of the above conjecture on noise is as follows. If Λ is evolutionarily stable and there is some small amount of noise perturbing the system, then with probability one, $\Lambda^\varepsilon_{p'} = U^\varepsilon$ for small enough ε. Thus, with noise, strong stability and this weaker notion are equivalent.

We distinguish interior ESAs from boundary ESAs. If p is an ESA value and the phenotypic constraint manifold is a smooth manifold near p then we say that the ESA is interior. If not then we say that it is a boundary ESA. We use this terminology because in our examples this occurs when P is an interval and one of the end-points of P gives an ESA.

We characterize the evolutionary stability of an attractor Λ_p for the pure dynamics with phenotype p by the invasion exponent $\vartheta_p(p') = \vartheta_p(\Lambda_p, p')$. This measures the rate of growth of small invading populations with phenotype p'. The dynamics of these invasions is, of course, given by the p'-mutated dynamics. The correct mathematical definition of ϑ is given in § 4. Misleading results occur if the precise form of this is not used, especially for chaotic attractors. We also derive some analytic expressions for it.

A positive growth rate ϑ means that a small population with phenotype p' will be able to invade and either take over or coexist with the original population. In our examples the principle of mutual exclusion holds which means that, after successful invasion, the invading population actually takes over and replaces the original population. Thus we observe evolution from p to p'. The magnitude of ϑ is related to the selective pressure and determines the speed at which the invasion initially takes place and hence the speed of the evolution. A negative ϑ implies that invasion by a small population with phenotype p' is impossible. The relation of ϑ to ESAs is given by the following theorem. For the precise hypotheses see § 4*a*.

Theorem 1.
1. If $\vartheta_p(\Lambda, p') < 0$ then Λ is evolutionarily stable to p'.
2. If $\vartheta_p(\Lambda, p') > 0$ then Λ is evolutionarily unstable to p'.
3. If $\vartheta_p(\Lambda, p') < 0$ for all $p' \neq p$ in P near p then Λ is evolutionarily stable. If there exists a sequence $p_i \to p$ such that $\vartheta_p(\Lambda, p_i) > 0$ then Λ is not evolutionarily stable.

When P is one-dimensional, in order to find ESAs numerically, it is useful to choose a small positive number ε and consider the functions† $f_+(p) = \vartheta_p(p+\varepsilon)$ and $f_-(p) = \vartheta_p(p-\varepsilon)$. These respectively measure the selective advantage of $p+\varepsilon$ and $p-\varepsilon$ over p. If $f_+(p) > 0$ then a small population with phenotype $p' = p+\varepsilon$ will be able to invade a p population. If mutual exclusion holds, then we get evolution to increasing values of p. If $f_+(p) < 0$, the invading population will die out. If $f_-(p) > 0$ then a small $p' = p-\varepsilon$ population will be able to invade the p population and if $f_-(p) < 0$, it will not. For small $\varepsilon > 0$, the zeros of these two functions approximate the interior ESAs in the following way: if for $p < p_*$, $f_+(p) > 0$ and for $p > p_*, f_-(p) > 0$ then this indicates that p_* is an ESA value. If the inequalities are the other way round, then we may regard p_* as an evolutionary repellor. If P is an interval then the right-hand (resp. left-hand) end-point is a boundary ESA value if $f_+ > 0$ (resp. $f_+ < 0$) near the end-point.

Because it is only necessary to consider one of f_+ or f_- to detect an ESA we will concentrate our attention upon f_+.

We illustrate these ideas by returning to our resource–predator–prey example (3). Suppose that our phenotype parameter p is b_1 or (b_1, c_1, c_2). Then in the first case only the prey are allowed to mutate while in the second both predator and prey can. And let us assume that there are no constraints on p. Then:

Proposition 1. There are no ESAs for the unconstrained system.

The reason is obvious but non-trivial to prove because of the complexity of the attractors of (3) and the proof is given in § 4*c*(ii). A prey with a given phenotype b_1

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† In fact, if $s(p)$ denotes the differential selective pressure defined below, then $f_+(p) \approx \varepsilon s(p)$. See equation (18).

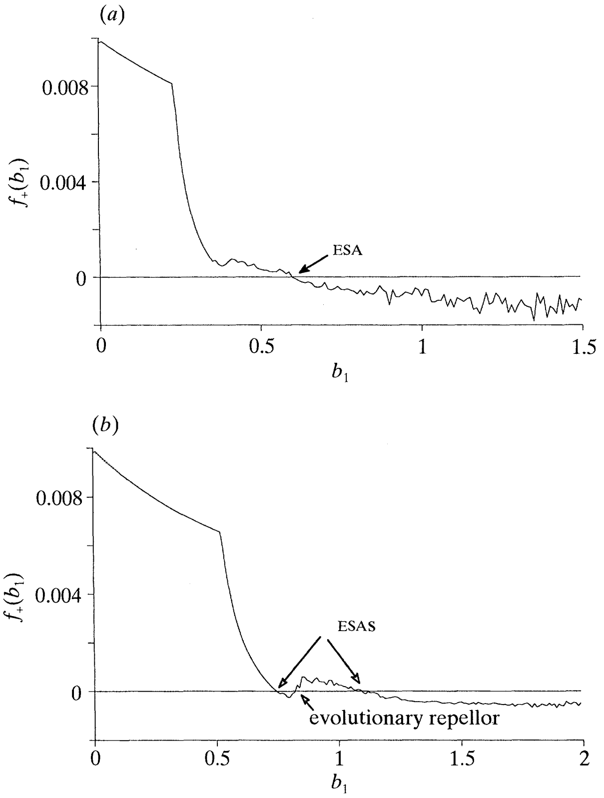

Figure 2. The graph of f_+ for equation (3) for parameter values corresponding to the two cases given in table 2. The jagged parts of the graph correspond to parameter values where the attractor is chaotic. The jaggedness is caused by the non-uniform convergence of time-series for the ergodic measures of chaotic attractors.

can always out-compete one with a slightly lower b_1. If we plot f_+ then we find that it is always positive. Clearly, to get evolutionary stability we need to introduce constraints.

Indeed, if the phenotype parameters are constrained then (3) does have an evolutionarily stable attractor. For example, it is natural to suggest a trade-off between the prey growth parameter b_1 and its contact parameter c_1 with the predator. It is sufficient that c_1 increases with b_1. For definiteness, we assume that c_1 is proportional to b_1. At the same time, for convenience, let us keep the ratio of c_2 to c_1 fixed. We regard the other parameters α, c_3, d_i as fixed. Thus our phenotype space P is given by

$$P = \{(b_1, c_1, c_2) : b_1 \geqslant 0, c_1/c_2 = k, b_1/c_1 = l\}, \qquad (8)$$

where $k = 1.7$ and $l = 440$ for the first set of parameter values and $k = 2.0$ and $l = 1100$ for the second set. The phenotype space is 1-dimensional and parametrised by $b_1 \geqslant 0$.

Proposition 2. If the parameter values (except b_1 which is variable) are as in table 1, this constrained system has at least one ESA value.

These attractors are chaotic. We will discuss this proposition further when we have introduced the invasion exponent in § 4 below.

A plot of f_+ for equation (3) for parameter values corresponding to the two cases given in table 2 is shown in figure 2. In the first case there is a single ESA value $p_* \approx 0.59$ and the corresponding ESA is chaotic. In the second there are two ESA values separated by an evolutionary repellor. One is a fixed point and corresponds to $p_\dagger \approx 0.75$. The other, which corresponds to $p_\ddagger \approx 1.1$, is chaotic. Thus we see that even in relatively simple systems we should expect multiple ESAS. Moreover, this and our other examples show that evolutionary stability and chaotic dynamics are perfectly compatible, as is any other common form of dynamical behaviour.

3. EVOLUTIONARILY STABLE STRATEGIES

One can show that if the dynamics are the mixed strategy population dynamics of linear evolutionary game theory, then the notion of an ESA coincides with the classical notion of an ESS. A slight complication is that, because the game dynamics are only frequency dependent the equilibrium populations are not attractors for the population dynamics. They are neutrally stable. Nevertheless, if this inessential fact is disregarded the theory is applicable and our approach allows a unified treatment of the various cases within this classical theory (such as playing the field and asymmetric competition) and also deals with a much wider range of nonlinear and dynamical situations. We illustrate this by considering a modification of the classical Hawk–Dove game (Maynard Smith 1982). In this the individuals are predators and the resource being competed for is a share of the prey population that is changing dynamically.

Table 3. *An explanation of the construction of equation (9)*

term in equation	interpretation
$1+b$	prey's unconstrained birth rate
$-\alpha\dfrac{x_1}{k}$	decrease in fitness of prey due to resource limitation
$-\dfrac{c_1 e_{12}}{1+d_1 e_{11}}$	decrease in fitness of prey due to predation
$e^{-\sigma}$	predator's unconstrained death rate
$\exp(c_2 E_{ij})$	payoff to an individual playing pure strategy i against an individual whose strategy is j
$E(p, e_{22})$	increase in fitness of predator playing the mixed strategy p in a population whose mean strategy is e_{22}

Table 4. *Scores and payoffs for the Hawk–Dove predator game with prey*

scores		payoff matrix		
win	$V = V_0 x_1$		H	D
injury	$-C$	H	$(V-C)/2$	V
loss	0	D	0	$V/2$

(*a*) *Game theory in a dynamic environment*

Recall the Hawk–Dove game as described in Maynard Smith (1982, chapter 2). We will suppose that the species playing a mixture of the two strategies Hawk and Dove is a predator and that the resource gained in each contest is a proportion V_0 of the prey population x_1. Thus the scores and payoff matrix are as shown in table 4. The main difference from the usual theory is that $V = V_0 x_1$ depends upon the number of prey x_1 and this is changing dynamically. If we denote the payoff matrix by $E = (E_{ij})$ and use the same notation as above, then our pure equations are‡

$$x_1' = x_1(1+b)\exp\left(-\alpha\frac{x_1}{k} - \frac{c_1 e_{12}}{1+d_1 e_{11}}\right),$$

$$x_2' = x_2\,\mathrm{e}^{-\sigma}E(p,e_{22}),$$

$$e = e(x\delta_p;p) = e(x\delta_p), \tag{9}$$

where $E(p,q) = \Sigma_{i,j}\, p_i q_j \exp(c_2 E_{ij})$, $e_{11}(\xi_1)$ is the total prey population $\int\xi_1(p_1)\mathrm{d}p_1$, $e_{12}(\xi_2)$ is the total predator population $\int\xi_2(p_2)\mathrm{d}p_2$ and $e_{22}(\xi_2)$ is the mean predator population strategy

$$\int p_2\xi_2(p_2)\mathrm{d}p_2 \Big/ \int \xi_2(p_2)\mathrm{d}p_2.$$

The biological interpretation of the various terms in the equation is given in table 3.

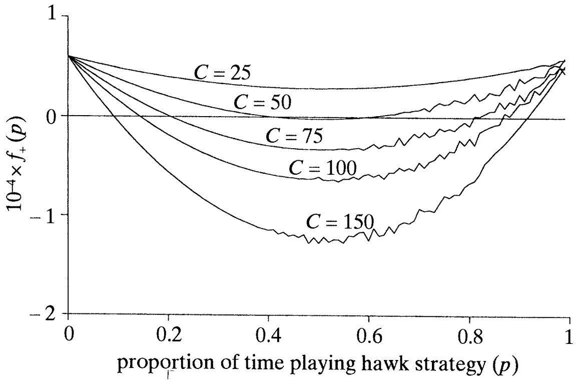

Figure 3. The graph of f_+ for the Hawk–Dove predator–prey system given by equation (9) for parameter values as given in table 5 and for variable injury cost C.

Note that in this case $e_{ij}(\xi_j)$ is a constant independent of p_i. We have included the death rate $-\sigma$ in the equation for the predators so that, without the increase in fitness gained by winning prey, their numbers would naturally decline.

It will be shown in § 4*c*(iii) that this system has an ESA at $p* = \bar{V}/C$ where $\bar{V} = V_0\bar{x}_1$ and $\bar{x}_1$ is the average value of x_1 with respect to the natural measure ν of the attractor for (9) when the phenotype is given by p ($\bar{x}_1 = \int x_1\nu(\mathrm{d}x)$). This fact is also clear from the graph of the function f_+ (see § 2) which was calculated numerically and is plotted in figure 3. This ESA corresponds to that for the classical linar game. However, it is also clear from this plot that there is a significant difference because $p = 1$ is also a boundary ESA value.

The reason for this can be clearly seen from figure 4 where we plot that the observed value of $\bar{V}/C$ against the proportion of Hawk behaviour. Since this proportion is equivalent to p, we use p to denote it. Note that one of the values p_* where the graph crosses the diagonal corresponds to the ESA and the other p_r to the evolutionary repellor. From the graph one can easily see the following: if p is less than p_* then the proportion of Hawk behaviour is less than $\bar{V}/C$ and therefore there is selective advantage to more hawkish behaviour. By similar reasoning, if p is greater than p_* and less that p_r then $p > \bar{V}/C$ and more dove-like behaviour

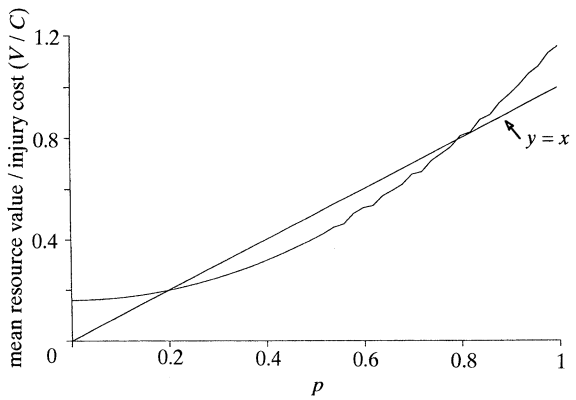

Figure 4. The graph of $\bar{V}/C$ against the proportion of Hawk behaviour, where the injury cost, C, is 75.

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‡ One aspect of our treatment of linear evolutionary games is non-standard. If the payoff to strategy i against strategy j is E_{ij}, then the contribution towards fitness is taken to be $\exp(cE_{ij})$ where c is some constant largely set by the timescale of the interactions. Then the mean fitness of an individual playing the strategy p in a population whose mean strategy is e is $E(p,e) = \Sigma_{i,j}\, p_i e_j \exp(cE_{ij})$. For discrete time dynamics this has a number of advantages while also giving the same ordinary differential equation as is usual for the continuous time dynamics. The advantages include: (i) natural positivity, unlike E_{ij}, $\exp(E_{ij})$ cannot be negative; (ii) invariance of the dynamics under addition of a constant to a column of the payoff matrix E_{ij}; and (iii) sensible scaling with the unit of time τ. For example, in the classical Hawk–Dove game $E_{HH} = (V-C)/2$ which can be negative, and this cannot be overcome by adding a constant to the fitnesses as this changes the classical version of the discrete-time dynamics as formulated in Maynard Smith (1982). Replacing the payoffs such as E_{HH} by terms of the form $\exp(cE_{HH})$ overcomes all these problems for mappings and preserves the continuous-time dynamics. The continuous-time dynamics are derived as follows: Assume that E_{ij} is the contribution to fitness over a small time period τ and that $c = \kappa\tau$. Let $W(p,e) = \Sigma_{i,j}\, p_i e_j \kappa E_{ij}$. Then,

$$x(t+\tau) - x(t) = \left(\sum_{i,j} p_i e_j \exp(\kappa\tau E_{ij} - 1)\right)x(t) = \tau W(p,e)x(t) + \mathcal{O}(\tau^2)$$

and therefore in the limit $\tau \rightarrow 0$ we obtain $\mathrm{d}x/\mathrm{d}t = W(p,e)x(t)$. This is the same differential equation as that obtained in Taylor & Jonker (1987) and Zeeman (1979). Finally, we stress that our preference for this formulation does not affect our conclusions in any important way.

Table 5. *Parameter values for the Hawk–Dove system given by equation (9)*

b	k_1	c_1	c_2	d_1	V_0	C		σ
0.5	1000	0.01	0.001	0.005	1.0	75	variable	0.006

is selected. But if p is greater than the evolutionary repellor then $p < \bar{V}/C$ and therefore more hawk-like behaviour is selected. This explains why $p = 1$ is a boundary ESA value.

For low p the system has a fixed point as its attractor while for larger values it has a quasiperiodic attractor. In this example the ESA is a fixed point.

Later in § 5*d* we will see that this example has particularly interesting phenotype dynamics for both the corresponding mixed strategy and polymorphic population problems. In the first case it has a highly structured asymptomatic distribution of strategies and, in the second, it displays complicated oscillatory behaviour.

4. THE INVASION EXPONENT

This section contains an important characterisation of evolutionary stability which provides the mathematical and computational tool for analysing examples. Since the full-blown definition for general attractors requires the use of less well-known mathematical tools (such as invariant measures), we start by discussing the simple case where the attractor Λ of our pure system is either a fixed point or a periodic orbit. After describing the results for such systems we consider the general case and chaotic attractors.

Firstly, we consider when an attractor Λ of the pure dynamics with phenotype p is stable to mutation from phenotype p to p'. The mutated dynamics are given by equation (6).

We may temporarily suppress the reference to p and p' as they are fixed for the present discussion. Let us also denote by y the vector (y_i) where the index i runs over those i such that $p'_i \neq p_i$. The equation (5) for the pure dynamics defines a mapping $x \mapsto x' = f(x)$ and equation (6) for the p'-mutated dynamics defines a mapping $(x,y) \mapsto (x',y') = g(x,y) = (g_1(x,y),\ g_2(x,y))$ where $g_1(x,0) \equiv f(x)$ and $g_2(x,0) \equiv 0$.

We are interested in determining whether or not there are small invading populations y which will grow under iteration of the mapping g. We show that such invasion is impossible if this is the case in the system where the equation for y is replaced by its linearisation. This defines what we call the variational mapping:

$$(x,y) \overset{V}{\mapsto} (f(x), T_x \cdot y), \tag{10}$$

where $T_x = d_y g(x,0)$ is the partial derivative of g with respect to y evaluated at $(x,0)$. Below we show how to calculate this for some important examples. The action of the mapping V on y is linear. Thus, we may expect that on average, under iteration, the length $\|y\|$ of y grows or decays exponentially fast. The exponential growth rate associated with a generic choice of y and x in the attractor Λ will provide us with our invasion exponent.

Now let us consider the simplest case where the attractor $\Lambda = \{x_0\}$ is just an attracting fixed point. Then the action of V on the x component is trivial and the map reduces to

$$y \mapsto T_{x_0} \cdot y,$$

where T_{x_0} is the linear map $d_y g(x_0,0)$. Thus we can apply standard theory to deduce that the behaviour is determined by the eigenvalues of T_{x_0}. If all the eigenvalues of T_{x_0} are inside the unit circle in the complex numbers $\mathbb{C}$ then the system is stable. We express this in the following way. Let λ denote the eigenvalue with largest modulus and let $\chi = \log|\lambda|$. Then the system is stable to invasion by a small population y with phenotype p' if $\chi < 0$ or equivalently, $|\lambda| < 1$.

A similar result holds if our attractor is a periodic orbit $x_0, \ldots, x_{q-1}$ of period q. Then we let λ be the eigenvalue with largest modulus of the product $T_{x_{q-1}} \ldots T_{x_0}$ corresponding to iterating once around the orbit. Again, the system is stable to small invasions if $\chi = \log|\lambda| < 0$.

To the attractor Λ of f and a mutated phenotype p' we are going to associate a number $\vartheta_p(\Lambda,p')$ which characterises the stability of Λ with respect to the mutation p'. In the simple cases above we would set

$$\vartheta_p(\Lambda,p') = \chi.$$

Then Λ is evolutionarily stable if for all $p' \neq p$ near p, $\vartheta_p(\Lambda,p') < 0$. Moreover, if $\vartheta_p(\Lambda,p') > 0$ for p' arbitrarily near p then it is evolutionarily unstable. We now want to extent this to general attractors and especially quasiperiodic and chaotic ones.

(*a*) *Definition of ϑ and its relation to evolutionary stability*

We can motivate our approach to this by noting that the number χ above is the growth rate of a typical y vector. This means that if $(x_n,y_n) = V^n(x,y)$, then $\|y_n\|$ grows like $\exp(n\chi)$ or more precisely that

$$\chi = \lim_{n \to \infty} \frac{1}{n} \log\|y_n\|.$$

We now generalize this idea to general attractors Λ.

Let T^n_x denote $T_{x_{n-1}} \circ \ldots \circ T_{x_0}$. We denote by $\|T^n_x\|$ the norm of T^n_x which is defined as

$$\|T^n_x\| = \sup_{y \neq 0} \frac{\|T^n_x \cdot y\|}{\|y\|}.$$

Then, a typical vector y grows at the same rate as $\|T^n_x\|$. Thus, in each of the above examples, $\chi = \lim_{n \to \infty} n^{-1}\|T^n_x\|$.

Now consider the general situation. With p' fixed let

$$\chi(x) = \chi_p(x,p') = \lim_{n \to \infty} \sup \frac{1}{n} \log\|T^n_x\|. \tag{11}$$

We will show that evolutionary stability is determined by the sign of $\chi(x)$ as x ranges over the attractor Λ.

The different values that $\chi(x)$ takes as x varies are given by the ergodic measures of Λ. For general attractors Λ, we must express our results in terms of these.

A probability measure ν is invariant if $\nu(f^{-1}(E)) = \nu(E)$ for all subsets E where $\nu(E)$ makes sense. An invariant measure is said to be ergodic if for all f-invariant sets E, $\nu(E)$ is either 0 or 1. This is equivalent to the following condition: for all continuous functions $v(x)$,

$$\lim_{n\to\infty} \frac{1}{n} \sum_{j=0}^{n-1} v(f^j(x)) = \int v(x)\nu(\mathrm{d}x),$$

for a set of x of full ν measure. Here, and in what follows, we denote the integral with respect to a measure ν of a function $v(x)$ over all x by $\int v(x)\nu(\mathrm{d}x)$.

The simplest example of an invariant measure ν occurs when $\Lambda = \{x_0\}$ is an attracting fixed point. Then, for ν, we take the delta function δ_{x_0} concentrated at x_0. It is invariant and ergodic because $\nu(E) \neq 0$ if and only if $x_0 \in E$. Similarly, if $\{x_0, \ldots, x_{q-1}\}$ is a periodic orbit of period q, the averaged delta function

$$\nu = (1/q) \sum_{i=0}^{q-1} \delta_{x_i}$$

is an ergodic invariant measure. And if Λ is an irrational invariant circle and $x \in \Lambda$ then

$$\nu = \lim_{q\to\infty} (1/q) \sum_{i=0}^{q-1} \delta_{f^i(x)}$$

is an invariant ergodic measure. In each case, there are no other invariant measures and the attractor is said to be uniquely ergodic.

However, for a chaotic attractor there exist uncountably many ergodic invariant measures. Often one of these has the property that for all continuous functions $v(x)$

$$\lim_{n\to\infty} \frac{1}{n} \sum_{j=0}^{n-1} v(f^j(x)) = \int v(x)\nu(\mathrm{d}x),$$

for a set of x of full Lebesgue measure in the basin of the attractor. There can only be one such measure and, if it exists, it is called the *natural measure* of Λ. It is clear that for each of the simple cases mentioned above the given ergodic measure is natural.

The following proposition follows from the subadditive ergodic theorem (Kingman 1976, Theorem 1.8; also see Ruelle 1979, Theorem 1.1 and Corollary) applied to $f_n(x) = \log\|T_x^n\|$.

Proposition 3. There exists a set $\Lambda_0 \subset \Lambda$ with the following properties.

(i) $\nu(\Lambda - \Lambda_0) = 0$ for all invariant probability measures ν.

(ii) If $x \in \Lambda_0$ then $\chi(x)$ exists as a limit i.e.

$$\chi(x) = \lim_{n\to\infty} \frac{1}{n} \log\|T_x^n\| = \inf_n \frac{1}{n} \log\|T_x^n\|. \tag{12}$$

(iii) $\chi(x)$ is f-invariant i.e. $\chi(f(x)) = \chi(x)$.

(iv) If ν is an ergodic invariant probability measure on Λ then there exists a set $\Lambda_\nu \subset \Lambda_0$ such that $\nu(\Lambda_\nu) = 1$ and for all $x,x' \in \Lambda_\nu$, $\chi(x) = \chi(x')$.

The last part of this proposition tells us that for each ergodic invariant probability measure ν,χ is constant almost everywhere and therefore given by a single number. We denote this by $\chi(\nu)$. By proposition 3,

$$\chi(\nu) = \int \chi(x)\nu(\mathrm{d}x).$$

Consider the approximations $\chi_n(x) = n^{-1} \log\|T_x^n\|$. In general, for chaotic attractors, the set of limit points of the sequence $\chi_n(x)$ as x ranges over the attractor Λ forms a closed interval $I_p(p') = [l_p(p'),r_p(p')]$. Moreover, in lemma 1, we will show that $l_p(p) = 1 = r_p(p)$. For fixed points, periodic orbits and quasiperiodic attractors, $I_p(p')$ is a single point because they are uniquely ergodic.

Theorem 2. Suppose that $r_p(p') < 0$. Then, for all $x \in \Lambda$, if $\|y\|$ is sufficiently small and if $(x_n,y_n) = g^n(x,y)$, $\|y_n\| \to 0$ as $n \to \infty$. If Λ is such that $I_p(p')$ consists of a single point $r_p(p')$ for all p' near p then Λ is evolutionarily stable in the strong sense if $r_p(p') < 0$ for all $p' \neq p$ near to p.

Unfortunately, if Λ is a chaotic attractor, it is only for very exceptional systems that $I_p(p')$ consists of a single point. We point out why in Appendix 2. This is part of the reason why for generic chaotic attractors the strong form of evolutionary stability cannot hold.

We will suppose that our attractor Λ has a natural measure ν_* and that this is absolutely continuous with respect to Lebesgue measure on unstable manifolds. We then define§

$$\vartheta_p(p') = \vartheta_p(\Lambda,p') = \chi(\nu_*) = \int \chi(x)\nu_*(\mathrm{d}x).$$

Since ν_* is a natural measure it follows that for x in some set of full Lebesgue measure in the basin of Λ,$\chi(x) = \vartheta_p(p')$.

Definition 3. $\vartheta_p(p')$ is called the *invasion exponent* of Λ for p'.

Theorem 1.

1. If $\vartheta_p(\Lambda,p') < 0$ then Λ is evolutionarily stable to p'.
2. If $\vartheta_p(\Lambda,p') > 0$ then Λ is evolutionarily unstable to p'.
3. If $\vartheta_p(\Lambda,p') < 0$ for all p' near p then Λ is evolutionarily stable. If there exists a sequence $p_i \to p$ such that $\vartheta_p(\Lambda,p_i) > 0$ then Λ is not evolutionarily stable.

The proof of this theorem which is very technical will be given in a separate paper.

(*b*) *Expressions for* ϑ *and coevolution*

We consider how the individual species groups contribute to the invasion exponent of the whole

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§ For obvious reasons we prefer the notation $\vartheta_p(p')$ to $\vartheta_p(\Lambda,p')$. However, the reader should be aware that it is possible that the pure system have two attractors Λ_1 and Λ_2. In this case, it is likely that $\vartheta_p(\Lambda_1,p') \neq \vartheta_p(\Lambda_2,p')$ in which case the notation $\vartheta_p(p')$ is ambiguous.

system. The result is summarized in proposition 4 and its corollary. En route we derive the important equation (15).

We start by calculating T_x. The equation for the mutants given by equation (6) is $y_i' X_i'(y,e_i,p')$ where $e_i = e_i(x,y,p,p';p_i') = e(x,p;p_i') + e_1(x,y,p,p';p_i') \cdot y$. Recall our standing assumption that if $y_i = 0$ then $y_i' = 0$. It follows that this equation must be of the form

$$y_i' = F_i'(y,e,p') \cdot y_i, \tag{13}$$

where $F_i'(y,e,p')$ is a linear operator. Note that the partial derivative with respect to y_j at $y = 0$ of the right-hand side of equation (13) is zero if $i \neq j$ because the right-hand side is divisible by y_i. Thus $T_x \cdot y = d_y g_2(x,0) \cdot y = y'$ where y_i' is given by (13). In other words, the ith component of $T_x \cdot y$ is given by

$$(T_x \cdot y)_i = T_{x,i} \cdot y_i,$$

where

$$T_{x,i} = F_i'(0,e(x,0),p'). \tag{14}$$

Therefore

$$\|T_x^n\| = \max_i \|T_{x,i}^n\|, \tag{15}$$

where $T_{x,i}^n = T_{f^{n-1}(x),i} \ldots T_{x,i}$. Let

$$\chi_i(x) = \chi_{i,p}(x,p') = \limsup_{n \to \infty} n^{-1} \log \|T_{x,i}^n\|,$$

and $\vartheta_{i,p}(p') = \chi_{i,p}(\nu*) = \int \chi_{i,p}(x)\nu*(\mathrm{d}x)$. Then by equation (15), $\chi(x) = \max_i \chi_i(x)$ and $\vartheta_p(p') = \max_i \vartheta_{i,p}(p_i') = \max_i \chi_i(\nu*)$. Thus we have proved:

Proposition 4. $\chi(x) = \max_i \chi_i(x)$ and $\vartheta_p(p') = \max_i \vartheta_{p,i}(p')$. In other words, the growth rate of a small invading population given by y is the maximum of the growth rates of the populations consisting solely of the individuals in this population which are in species group i. A mixed population only invades as fast as the species groups that it is made up of.

Corollary 1. Λ is evolutionarily stable to p' if for each i such that $p_i' \neq p_i$, $\vartheta_{i,p}(p_i') < 0$, i.e. if it cannot be invaded by a group consisting solely of the individuals in the population which are in species group i.

(*c*) *Nonlinear criteria for* ESA*s and selective pressure*

We start with the remark about cross-term constraints on the phenotype which was promised in § 2*a*(ii).

Remark 1. Cross terms arise in interactions involving the jth phenotype in the ith equation. An example is the term e_{12} in equation (3). But, by equation (14), $T_{x,i}$ only depends upon x, $e(x,p;p_i')$ and p' and all cross-terms have to enter through e. In particular, the dependence upon p' is only through p_i'. As in § 2*a*(ii), let q_i denote the vector of all those parameters and interactions which depend upon p_i and let q_i' denote the value corresponding to p'. Then $T_{x,i}$ only depends upon x, p and q_i' and we write $T_{x,i} = T_{x,i}(p,q_i')$. This fact is used in what follows.

(i) *Differential selective pressure*

We now consider the case where y_i is a scalar.[‖] This is the case for all our examples. Then $T_{x,i}$ is just multiplication by a scalar. As we noted in the above remark, as far as the dependence of $T_{x,i}$ upon p' is concerned it only depends upon q_i'. We define $\theta_i(x,q_i') = \theta_{i,p}(x,q_i') = \log|T_{x,i}|$. Then

$$\chi_i(x) = \limsup_{n \to \infty} \frac{1}{n} \sum_{j=0}^{n-1} \theta_i(f^j(x),q_i').$$

where the lim sup is a limit if $x \in \Lambda_0$. Moreover, if ν is an invariant measure,

$$\chi_i(\nu) = \int \theta_i(x,q_i')\nu(\mathrm{d}x),$$

is the value of $\chi_i(x)$ for a set of x of full ν-measure in Λ. Note that $\chi_i(x)$ and $\chi_i(\nu)$ depend upon both p and q_i'. The dependence upon p comes from the cross-terms and also the averaging over x using ν.

Fix p and the corresponding pure attractor Λ which is not necessarily an ESA. Expand $\theta(x,q_i') = \theta_i(x,q_i') = \log|T_x|$ as follows using Taylor's Theorem:

$$\begin{aligned}\theta(x,q_i') = {} & \theta(x,q_i) + d_{q_i}\theta(x,q_i) \cdot (q_i' - q_i) \\ & + \frac{1}{2} d_{q_i'}^2\theta(x,q_i) \cdot (q_i' - q_i)^2 + \mathcal{O}((q_i' - q_i)^3).\end{aligned} \tag{16}$$

Thus,

$$\begin{aligned}\int \theta(x,q_i')\nu(\mathrm{d}x) = {} & \int \theta(x,q_i)\nu(\mathrm{d}x) + \left(\int d_{q_i}\theta(x,q_i)\nu(\mathrm{d}x)\right) \cdot \\ & (q_i' - q_i) + \left(\frac{1}{2}\int d_{q_i'}^2\theta(x,q_i)\nu(\mathrm{d}x)\right) \cdot (q_i' - q_i)^2 \\ & + \mathcal{O}((q_i' - q_i)^3).\end{aligned}$$

Lemma 1. If each y_i is either one-dimensional or an age-structured population in the sense of Appendix 2, then $\chi_{i,p}(x,q_i) = \lim_{q_i' \to q_i} \chi_{i,p}(x,q_i') = 0$. In the one-dimensional case, this is equivalent to $\chi_i(\nu) = \int \theta(x,q_i)\nu(\mathrm{d}x) = 0$ for all invariant measures ν on Λ.

The proof of this lemma is given in Appendix 2. It follows immediately that the first term of the right-hand side of the previous equation is zero. Then, if ν_* is the natural measure,

$$\begin{aligned}\vartheta_{i,p}(q_i') = {} & \left(\int d_{q_i}\theta(x,q_i)\nu_*(\mathrm{d}x)\right) \cdot (q_i' - q_i) \\ & + \left(\frac{1}{2}\int d_{q_i}^2\theta(x,q_i)\nu_*(\mathrm{d}x)\right) \cdot (q_i' - q_i)^2 + \mathcal{O}((q_i' - q_i)^3), \\ = {} & s_i(p) \cdot (q_i' - q_i) + \frac{1}{2} s_i'(p) \cdot (q_i' - q_i)^2 + \mathcal{O}((q_i' - q_i)^3).\end{aligned} \tag{17}$$

Definition 4. We call $s_i(p) = \int d_{q_i}\theta_i(x,q_i)\nu_*(\mathrm{d}x)$ the differential selective pressure[¶] of the ith species group. The differential selective pressure of the ecology is the function $s(p) = (s_0(p), \ldots, s_s(p))$.

[‖] Analogous results can be proved for the case where y_i is an age structured vector. However, in this case, the analytic dependence of $\vartheta_p(p')$ on p' has a more complex proof and its derivative with respect to p' has a more complicated formula.

[¶] In a later paper (Rand 1993) we will argue that the selective pressure should be understood as a 1-form on the phenotype space. This approach clarifies the meaning of fitness in complex dynamical ecologies and aids calculations of evolutionary stability and instability in such situations.

Let Q_i denote the set of values taken by the parameters q_i as p_i varies over P_i. When $q_i = p_i$, as is often the case, then $Q_i = P_i$. We now make the reasonable assumption that for all $q_i \in Q_i$ there is a $p \in P$ such that q_i is the value corresponding to p.

Let d_i be the dimension of Q_i. Then $s_i(p)$ is a linear mapping from $\mathbb{R}^{D_i}$ to $\mathbb{R}$. The set of such mappings is equivalent to $\mathbb{R}^{D_i}$. Thus s_i can be thought of as a mapping from P to $\mathbb{R}^{D_i}$. The second derivative $d^2_{q_i}\theta(x,q_i)$ is given by a $d_i \times d_i$ symmetric matrix. Thus

$$s_i'(p) = \int d^2_{q_i'}\theta(x,q_i)\nu_*(\mathrm{d}x),$$

is given by a $d_i \times d_i$ symmetric matrix $M = M_i$. We say that this is negative definite if for all d_i-dimensional vectors $v \neq 0, M \cdot (v,v) = v^tMv < 0$. In the case where $d_i = 1$, this just means that the scalar quantity $s_i'(p)$ is negative.

If Λ is an interior ESA, then we must have $s_i(p) = 0$ for all i. Otherwise, by (17), for some i, $\vartheta_{p,i}(q_i')$ would be positive for some q_i' near q_i in Q_i. Conversely, if $s_i(p) = 0$ and $s_i'(p)$ is negative definite for all i, then $\vartheta_{p,i}(q_i')$ has a maximum at the value of q_i corresponding to p for all i, and therefore Λ is an ESA. Because this is important, we sum it up in a theorem.

Theorem 3. If p is an interior point of P, Λ is an ESA if, for all i, $s_i(p) = 0$ and $s_i'(p)$ is negative definite. Conversely, if Λ is an ESA then $s_i(p) = 0$ for all i.

Note that as p is interior, it is implicitly assumed that P is a smooth manifold near p and that each s_i is smooth near p. In solving $s(p) = 0$ it is only necessary to check $s_i(p) = 0$ for all species groups i that can mutate. Species groups that are for some reason constrained to the pure phenotype value p can be ignored for this purpose.

In the equation $s(p) = 0$, each term $s_i(p)$ can be considered as an element of $\mathbb{R}^{d_i}$, i.e. is d_i-dimensional. Thus $s(p)$ is d-dimensional where $d = \Sigma_i\, d_i$. In general, dim $P \geqslant d$ so that it is reasonable to expect $s(p) = 0$ to have solutions. If we choose $p = q$ (see the discussion of phenotypic redundancy in § 2*a*(ii)), then dim $P = d$, our equations are balanced and we expect that, generically, any solutions of $s(p) = 0$ will be isolated points.

We note that for the following cases $s_i(p)$ is simply found: (i) for a fixed point $\Lambda = \{x_0\}$, $s_i(p) = \max_i d_{q_i'}\theta_{i,p}(x_0,q_i)$; (ii) for a periodic orbit $\Lambda = \{x_0, \ldots, x_{n-1}\}$,

$$s_i(p) = n^{-1}\sum_{j=0}^{n-1} d_{q_i'}\theta_{i,p}(x_j,p_i);$$

and (iii) for a quasiperiodic attractor

$$s_i(p) = \lim\nolimits_{n\to\infty} n^{-1}\sum_{j=0}^{n-1} d_{p_i'}\theta_{i,p}(f^j(x),q_i),$$

if $x \in \Lambda$.

Consider the case where $P = P_i$ is one-dimensional and a single species group is mutating. If $s(p) = s_i(p) > 0$ for $p \in P = P_i$ then for p' slightly larger than p, $\vartheta_p(p') > 0$. Thus, if the principle of mutual exclusion holds (as it does in our examples), then one will observe evolution away from p towards higher values. Moreover, we observe that in this one-dimensional case the functions $f_+(p)$ and $s(p)$ effectively determine each other. By equation (17),

$$\vartheta_{p,i}(x,p') = s(p) \cdot (p' - p) + \mathcal{O}((p' - p)^2).$$

Therefore, since $f_+(p) = \theta_i(p + \varepsilon)$,

$$f_+(p) = s(p) \cdot \varepsilon + \mathcal{O}(\varepsilon^2). \tag{18}$$

Thus in calculating $f_+(p)$, as in § 2*b*, we have effectively calculated $s(p)$.

To illustrate the ideas of this section and the generic form of $\vartheta_p(p')$ when p is an ESA value, we use these facts to analyse the resource–predator–prey and Hawk–Dove models.

(ii) *ESAs in the resource–predator–prey model*

We consider why propositions 1 and 2 are true. The equation for the mutant prey y is $y'/y = \phi(x,y,p')$ where

$$\phi(x,y,p') = (1 + b)\exp\left(-\alpha\frac{x_1 + y}{x_3} - c_1\frac{x_2}{1 + d_1(x_1 + y)}\right),$$

and $b = b_1$ and the other parameters are functions of p'. Thus $\|T_x\| = \phi(x,0,p')$ and therefore

$$\theta(x,p') = \theta_1(x,p') = \log(1 + b) - \alpha\frac{x_1}{x_3} - c_1\frac{x_2}{1 + d_1x_1}.$$

In the unconstrained case,

$$d_b\theta(x,p') = (1 + b)^{-1} > 0.$$

Thus, if p' differs from p only in having a larger b value, then the system is unstable to p'.

On the other hand, for the constrained system of proposition 1,

$$\theta(x,p') = \log(1 + b) - \alpha\frac{x_1}{x_3} - \frac{b}{l}\frac{x_2}{1 + d_1x_1},$$

where $l = 440$ for the first set of parameter values of table 2 and $l = 1100$ for the second set. Therefore,

$$d_b\theta(x,p') = (1 + b)^{-1} - \frac{x_2}{l(1 + d_1x_1)}.$$

Let $\mu = l^{-1}\int x_2(1 + d_1x_1)^{-1}\nu_*(\mathrm{d}x)$. Then

$$s(b) = \int d_b\theta(x,p')\nu_*(\mathrm{d}x) = (1 + b)^{-1} - \mu,$$

whence $s(b) = 0$ if $b = \mu^{-1} - 1$. Because $0 < \mu \leqslant 1$,

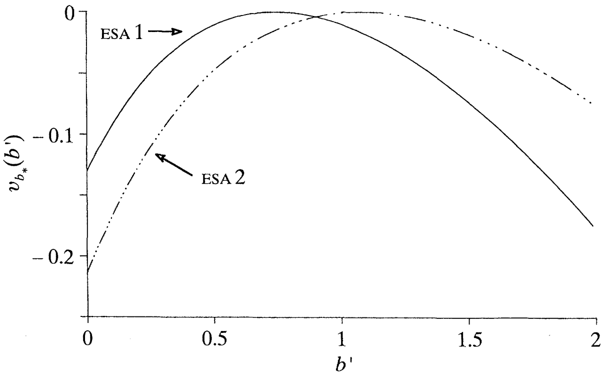

Figure 5. A plot of the function $\vartheta_{b*}(b')$ for the two ESA values of the resource–predator–prey model corresponding to the second set of parameter values in table 2.

there is such a value. Call it b_*. Moreover, as $d_b^2\theta(x,b_*) = -(1+b_*)^{-2} < 0, s'(b_*) = -(1+b_*)^{-2} < 0$. Consequently, this value corresponds to an interior ESA for the constrained system. Note that this argument does not exclude the possibility of more than one ESA.

In figure 5 we show the graphs of ϑ_p for the two ESA values p for the second set of parameter values.

(iii) *ESAs in the Hawk–Dove predator–prey system*

We now consider the Hawk–Dove predator game with dynamic prey as discussed above in § 3*a*. For this example, $y'/y = \phi(x,y,p')$ where $\phi(x,p') = \phi(x,0,p')$ is given by

$$\phi(x,p') = e^{-\sigma}\sum_{i,j} p_i'p_j \exp(cE_{ij}),$$

$$= \exp\left(-\sigma + c\sum_{i,j} p_i'p_jE_{ij}\right) + \mathcal{O}(c^2),$$

as

$$\sum_{i,j} p_i'p_j = 1.$$

Thus, ignoring terms which are of order c^2,

$$\theta(x,p') = -\sigma + c\sum_{i,j} p_i'p_j E_{ij}.$$

Because $p = (h,d)$ where h is the proportion of time playing Hawk and $d = 1 - h$,

$$\theta = -\sigma - (C/2)\,hh' + (V/2)\,(h' - h) + (V/2),$$

where $V = V_0x_1$. Thus $d_{p'}\theta(x,p') = -Ch/2 + V/2$ and $\int d_{p'}\theta = -Ch/2 + V_0\bar{x}_1/2$ where $\bar{x}_1 = \int x_1\nu_*(\mathrm{d}x)$. It follows that

$$s(p) = (1/2)\,(V_0\bar{x}_1 - Ch).$$

Thus $s(p) = 0$ if for the natural measure $\nu*$ for the phenotype p,

$$h = V_0\bar{x}_1/C.$$

However, in this case $d_{h'}^2\theta \equiv 0$, and therefore for this value of p,

$$s'(p) = 0. \tag{19}$$

(iv) *The generic structure of $\vartheta_p(p')$*

The degeneracy expressed by equation (19) is a result of the linear dependence of the payoff upon p'. For this linear game theory, it is the reason why it is necessary to use the second-order condition in the ESS criterion (equation (2.4) of Maynard Smith 1982). For general nonlinear games or dynamical systems such second-order conditions are not needed. This is illustrated by the previous example. For such generic cases, we observe that if p is an ESA value then the invasion exponent function $\vartheta_p(p')$ has a quadratic maximum at p where it takes the value 0. This is the situation shown in figure 5.

(*d*) *The invasion exponent for Lotka–Volterra systems*

Following Hofbauer *et al.* (1987), we consider the class of systems given by

$$x_i' = x_i \exp\left\{r_i - \sum_{j=1}^{d} a_{ij}x_j\right\} \qquad (i = 1, \ldots, d).$$

We refer to these as Lotka–Volterra mappings. We show that for these systems, the invasion exponent is given by the value of θ at a fixed point even when the attractor is chaotic. A similar result holds for Lotka–Volterra odes.

In our formalism the pure equation is given by

$$x_i' = x_i \exp\left\{r_i - \sum_{j=1}^{d} a_{ij}e_{ij}\right\} \qquad (i = 1, \ldots, d). \tag{20}$$

where $e_{ij}(\xi_j)$ is of the form $\int\alpha(p_j)\xi_j(p_j)\mathrm{d}p_j$ where $\alpha(p_j)$ is any smooth function of p_j and the parameters $r_i = r_i(p)$ and $a_{ij} = a_{ij}(p)$ are functions of the phenotype p.

We assume throughout this section that our attractor Λ is bounded away from 0 and ∞ in the following sense: there exists $K > 0$ such that for all $x \in \Lambda$, $K^{-1} < \|x\| < K$.

We now prove the following result:

Proposition 5. For such Lotka–Volterra systems $\vartheta_p(\Lambda,p') = \max_i \phi_i(\bar{x})$ for some fixed point $\bar{x}$.

This result makes it particularly easy to check the evolutionary stability of Lotka–Volterra attractors even if they are chaotic.

Proof. If $x \in \Lambda$, consider

$$\bar{x}^n = \frac{1}{n}\sum_{j=0}^{n-1} f^j(x).$$

Now, if $x^n = (x_1^n, \ldots, x_d^n) = f^n(x)$,

$$\frac{1}{n}\log\frac{x_i^n}{x_i^0} = \frac{1}{n}\sum_{k=1}^{n-1}\psi_i(f^k(x)),$$

where $\psi_i = r_i - \sum_{j=1}^{d} a_{ij}x_j$.

Thus

$$\frac{1}{n}\log\frac{x_i^n}{x_i^0} = r_i - \sum_{j=1}^{d} a_{ij}\bar{x}_j^n.$$

Because Λ is bounded away from 0 and ∞, the left-hand side converges to 0 as $n \to \infty$. Thus, if $\bar{x}$ is a limit point of the sequence $\bar{x}^n$, then $\psi_i(\bar{x}) = 0$ for all i and therefore $\bar{x}$ is a fixed point of (20).

The linear operator $T_{x,i}$ is just multiplication by $\exp(\phi_i(x))$, where $\phi_i(x) = r_i' - \Sigma a_{ij}' e_i(x,p) = r_i' - \Sigma a_{ij}'\alpha(p)x_i$ and $r_i' = r_i(p')$, $a_{ij}' = a_{ij}(p')$. Therefore, if $y_i^n = T_{x,i}^n \cdot y_i^0$,

$$\alpha_n = \frac{1}{n}\log\frac{y_i^n}{y_i^0} = \frac{1}{n}\sum_{j=1}^{n-1}\phi_i(f^j(x)) = \phi_i(\bar{x}^n),$$

as ϕ_i is affine in x. Thus, if $\bar{\alpha}$ is a limit point of the sequence α_n, there exists a subsequence n_i such that the two limits

$$\bar{\alpha} = \lim_{i\to\infty}\phi_i(\bar{x}^{n_i}),$$

and $\bar{x} = \lim_{i\to\infty} \bar{x}^{n_i}$. exist. Thus,

$$\bar{\alpha} = \phi_i(\bar{x}).$$

But, by the above, $\bar{x}$ is a fixed point of (20). Taking

$$\bar{\alpha} = \chi_i(x) = \limsup_{n\to\infty} \frac{1}{n} \log\|T^n_{x,i}\| = \limsup_{n\to\infty} \phi_i(\bar{x}^n),$$

we deduce that

$$\chi_i(x) = \phi_i(\bar{x}),$$

where $\bar{x}$ is a limit point of $\bar{x}^n$ and hence a fixed point of (20).

This proves that all limit points of $n^{-1}\log\|T^n_{x,i}\|$ are of the form $\phi_i(\bar{x})$ for some fixed point.

(*e*) *Numerical calculation of* ϑ

Assuming that one knows the equations of motion, the simplest way to numerically compute ϑ is to use the definition directly. One computes

$$T^n_{x,i} = \prod_{j=0}^{n-1} F'_i(0,e(x,p;p'_i),p'),$$

along an orbit $x_n = f^n(x)$ and finds its largest eigenvalue $\lambda_{i,n}$. Then, for large n, ϑ is estimated by $\max_i \vartheta_i$ where ϑ_i is estimated by $n^{-1}\log\lambda_{i,n}$. A more reliable estimate of ϑ_i is obtained by plotting $\lambda_{i,n}$ against n and making a least-squares estimate of its slope but this requires more numerical effort. As a compromise one can do this only for a subset of the set of n.

If F_i is given by a primitive age structure matrix as in Appendix 2, then all of the non-zero entries a^n_{ij} of $T^n_{x,i}$ have the same growth rate which equals ϑ_i. Thus we can use this to estimate ϑ_i and avoid the calculation of eigenvalues. We estimate ϑ_i by the slope of the graph of a^n_{ij} as a function of n. In this case a least-squares estimate is practical.

When y_i and hence $F'_i(0,e(x,p;p'_i),p')$ is a scalar, let

$$\theta_i(x,p') = \log F'_i(0,e(x,p;p'_i),p').$$

Then to estimate ϑ_i plot the sums

$$\theta^n(x,p') = \sum_{j=0}^{n-1} \theta_i(x_j,p')$$

against n and estimate the slope.

Finally, we describe another way to calculate ϑ. We describe this in the context where we have the equations of motion. Recall that we denote by f the mapping defined by the equation (5) for the pure dynamics Equation (6) for the p'-mutated dynamics defines the mapping $(x,y) \to (x',y') = g(x,y) = (g_1(x,y), g_2(x,y))$ where $g_1(x,0) \equiv f(x)$ and $g_2(x,0) \equiv 0$.

Firstly, we fix a small number $d > 0$ and a fixed multiple $D = md$ of d. Given $x_0 \in \Lambda$, let $x_i = f^i(x_0)$. Given a y vector y_0 of length d, we then define a sequence z_i of y vectors as follows. Let $z_0 = y_0$. If $\|z_i\| < D$ then we set $z_{i+1} = g_2(x_i,z_i)$. Otherwise, we set $z_{i+1} = g_2(x_i,z'_i)$ where $z'_i = dz_i/\|z_i\|$. In the latter case, or if $i = 0$, we call i a jump value. Corresponding to each jump value i we associate a number

$$d_i = d_{i-1} + \log\frac{\|z_j\|}{d},$$

where $j > i$ is the next jump value. Then ϑ is approximated by the slope of the best fitting straight line through the set of points.

$$\{(i,d_i) : i \text{ a jump value}\},$$

when d is taken very small.

5. PHENOTYPE DYNAMICS

We now consider the dynamics on phenotype space implied by the system consisting of both the pure dynamics and the interactions. A distribution of phenotypes is present in the population and we study the way in which it changes in time. Recall that the phenotypic constraint manifold P is a subset of the product $P_1 \times \ldots \times P_s$ of the s phenotype manifolds $P_1, \ldots, P_s$ corresponding to the s different species groups. We let $x_i(p_i)$ denote the phenotypic density of individuals in species group i i.e. $x_i(p_i)dp_i$ is the number of individuals in species group i whose phenotype lies in a volume dp_i based at p_i.

(i) *Mutation-free dynamics*

The (mutation-free) dynamics are then given by

$$x'_i(p_i) = X_i(x(p),e_i,p),$$
$$e_i = e_i(x;p_i), \qquad (21)$$

where X_i is given by the pure dynamics equation (5), $x(p) = (x_1(p_1), \ldots, x_s(p_s))$, $p = (p_1, \ldots, p_s)$ and $e(x;p_i)$ is the value of the interactions corresponding to the distribution given by x.

This defines a dynamical system on the space of functions of the form $x(p) = (x_1(p), \ldots, x_s(p))$. Let us denote the mapping given by this by L, i.e. $L(x) = x'$.

The pure dynamics (5) follow from equation (21) by taking for x_j the distribution $x_j^0\delta_{pj}$ for each j where δ_{pj} is the delta function on P_j concentrated at p_j (i.e. each species group j is represented by a single population of x_j^0 individuals each with the phenotype p_j). The p'-mutated dynamics (6) are then also given by (21) by taking for x_j the distribution $x_j^0\delta_{p_j}$ if $p'_j = p_j$ and $x_j^0\delta_{p_j} + y_j^0\delta_{p'_j}$ when $p'_j \neq p_j$.

(ii) *Mutations*

Now, we consider how to add mutations to this process. We discuss this in terms of distributions on the phenotype space. These represent the distribution of the phenotypes present in the system. In the pure case where only a single phenotype p_j is present in species group j, this is represented by a delta function δ_{p_j}. We assume that under mutation in group j such a pure situation changes to the probability distribution $M_j(\delta_{p_j})$. This means that after one time step, mutation causes the distribution of phenotypes to change from δ_{p_j} to $M_j(\delta_{p_j})$. Usually, $M_j(\delta_{p_j})$ will be a smooth distribution close to the delta function δ_{p_j}. Now we can use this to consider how a general population given by $x(p) = (x_1(p_1), \ldots, x_s(p_s))$ is changed by mutation to $M(x)(p)$. Because $x_j(p_j) = \int x(q_j)\delta_{p_j}\mathrm{d}q_j$, the general mutation is given by

$$M_j(x_j)(p_j) = \int x(q_j)(M(\delta_{q_j})(p_j))\mathrm{d}q_j. \tag{22}$$

Note that M_j is a linear operator. Now if $x = x(p)$ then the phenotype dynamics are given by $F(x) = M(L(x))$ i.e.

$$x \xrightarrow[\text{local dynamics}]{L} L(x) \xrightarrow[\text{mutation process}]{M} M(L(x)),$$

where

$$M(x)(p) = (M_1(x_1)(p_1), \ldots, M_s(x_s)(p_s)).$$

(*a*) *Game dynamics*

Before proceeding we note that, in the case of linear evolutionary games as in § 3 above, we obtain the Hines–Jonker–Taylor–Zeeman dynamics. Recall that the pure dynamics for this system is given by,

$$x' = xE(p,e),$$

$$e = e(x\delta_p, p) = p,$$

where the interaction e is the mean population strategy. (Note that $e = e(x,p;\pi)$ is independent of π in the case.) The phenotype vector is $p = (p_1, \ldots, p_s)$. Thus the mutation-free phenotype dynamics are given by

$$x(p)' = x(p)E(p,e),$$

$$e_i = \text{mean population strategy} = \frac{1}{N}\int p_i x(p)\mathrm{d}p,$$

where N is the total population $\int x(p)\mathrm{d}p$. We deduce that

$$v'(p) = \alpha E(p,e)v(p),$$

where $v(t) = x(t)/N$ gives the strategy frequencies, e is the mean strategy and α is a normalising factor keeping the total probability mass fixed at 1, i.e.

$$\alpha^{-1} = \int E(p,e)\mathrm{d}p = \int\int E(p,q)v(q)\mathrm{d}q\,\mathrm{d}p. \tag{23}$$

This is the equation given in equation 4.1 of Hines (1987) and Zeeman (1981) for the dynamics of a distribution of mixed strategies.

Hines (1980) showed that if p is an equilibrium for the Taylor–Jonker dynamics then any distribution v with mean p is an equilibrium for the above dynamics. Furthermore, he proved that the mean p is stable with respect to all mixed strategy perturbations v if and only if p is an ESS. Zeeman (1981) reinterpreted this by directly looking at the dynamic on the infinite dimensional space of measures on the simplex.

(*b*) *Computational methods*

The implementation of the phenotype dynamics involves the discretisation of the phenotypic constraint manifolds P_i. If they are one-dimensional then we approximate them by only considering an equally spaced lattice of phenotypes p_i^j, $j = 1, \ldots, N$. We denote the spacing by $\alpha = \alpha(P)$ and always check that our results are not dependent upon the particular choice of α. The phenotypic population distribution $x_i(p_j)\mathrm{d}p_j$ is then approximated by the vector $(x_i(p_i^1), \ldots, x_i(p_i^N))$. (Strictly these entries should be scaled by the volume which is a power of α, but this makes no difference and is only relevant if one is interested in taking the continuum limit.) The interactions e_{ij} which are all integrals over $\mathrm{d}p_j$ in the examples that we consider then become sums.

The mutation process is taken to be of the following form

$$M_j(\delta_{p_j^k}) = \frac{1}{Z}\sum_{l=-c}^{c} \lambda^{|l|}\delta_{p_j^{k+l}}, \tag{24}$$

where Z is a normalising factor chosen to ensure that $M_j(\delta_{p_j}^k)$ defines a probability distribution and $0 < \lambda < 1$. The parameter λ is the mutation rate. Of course, in this discretized situation, the delta function $\delta_{p_j^l}$ is just represented by the vector in $\mathbb{R}^N$ all of whose entries are zero except that corresponding to the lth entry.

In all the cases treated here we take $c = 1$.

(*c*) *Phenotypic attractor for the constrained resource–predator–prey model*

Recall that in this constrained problem we only allow the phenotype of the prey to vary. Thus only b_1, c_1 and c_2 vary and these are related so that the phenotype $p = p_1$ is determined by b_1 and hence identified with it. Therefore, the discretized phenotype dynamics for the resource–predator–prey system whose pure dynamics and interactions are given by equation (3) are

$$\begin{aligned}
\frac{(x_1^l)'}{x_1^l} &= (1 + b_1)\exp\left(-\alpha\frac{e_{11}}{e_{13}} - \frac{e_{12}^l}{1 + d_1e_{11}}\right),\\
\frac{x_2'}{x_2} &= (1 - d_2)\exp(e_{21}),\\
\frac{x_3'}{x_3} &= (1 + b_3)\exp\left(-\frac{e_{33}}{k} - e_{31}\right),
\end{aligned} \tag{25}$$

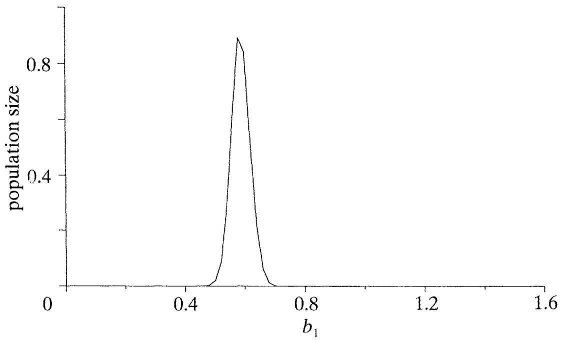

Figure 6. The asymptotic distribution for the phenotype dynamics of the resource–predator–prey system whose pure dynamics are given by equation (3) with parameter values from the first set in table 2.

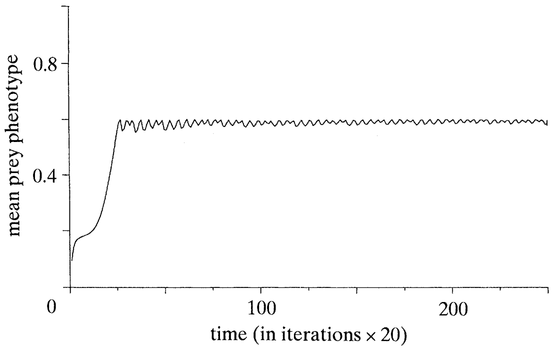

Figure 7. Time dependence of the mean phenotype showing convergence to the ESA value.

$$e_{ij} = \text{population size of species group } j = \sum_l x_j^l \qquad (ij = 11, 13 \text{ and } 33),$$

$$e_{ij} = \text{species group } j \text{ population mean of } c_i = \sum_l c_i^l x_j^l \qquad (ij = 21 \text{ and } 31).$$

Here $x_i^l = x_i(p_i^l)$ and $c_j^l = c_j(p_j^l, p_i^l)$. As we are only allowing the prey's phenotype to change, $e_{13} = e_{33} = x_3$ and

$$e_{12}^l = c_1^l x_2.$$

The parameter values are as in table 2. Recall that for the first set of values, there is a single ESS at $p = p*$. There is a distribution $\xi_1(p_1^l)$ such that, under the phenotype dynamics (with the mutation process defined by equation (22)), any initial distribution converges to $\xi_1(p_1^l)$. This asymptotic distribution is a 'smoothed out' delta function and is shown in figure 6. Note that it is very much wider than the mutated delta function $M_1(\delta_{p*})$. In figure 7 we show the time dependence of the mean phenotype. It shows convergence to the ESA value.

Not surprisingly in the second case, where there are two ESA values separated by an evolutionary repellor, the behaviour is more complicated. Any initial condition converges to one of two asymptotic distributions, but to which depends upon the initial condition and the mutation rate. If the latter is relatively large, then the asymptotic state is always a 'smoothed out' delta-function close to the larger ESA value as in figure 8. If the mutation rate is smaller and the support of the initial condition is very close to the smaller ESA value or to the left of this, then the asymptotic state is a 'smoothed out' delta function close to this ESA value. This is also shown in figure 8. Otherwise, it converges to the other asymptotic state.

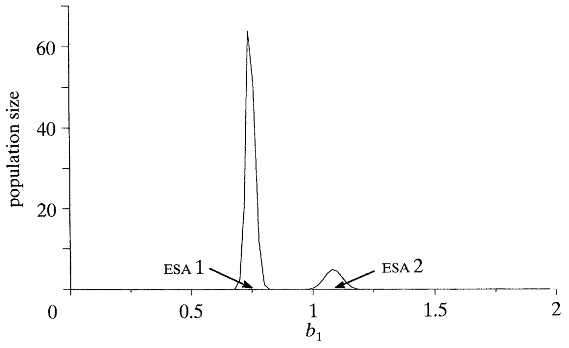

Figure 8. The two asymptotic distributions for the second set of parameter values in table 2 for the resource–predator–prey system.

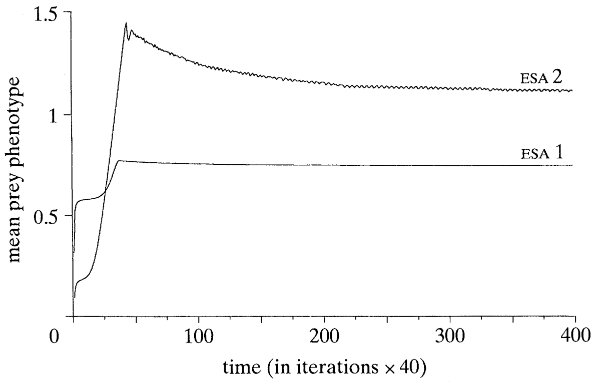

Figure 9. Time dependence of the mean phenotype showing convergence to the two ESA values.

In figure 9 we show the time dependence of the mean phenotype for an initial condition which depending on the size of the mutation rate converges to one of the two asymptotic distributions. The phenotypes present in the initial condition are all to the left of the smaller ESA value.

(*d*) *Phenotype dynamics for the Hawk–Dove predator–prey system of* § *3a*

(i) *Mixed strategies*

Recall that we studied this in § 3*a* for the case where each predator played a mixed strategy. We therefore consider the phenotype dynamics for this case first before proceeding to the case of a polymorphic population.

It follows from the definition of the pure dynamics and the interactions that the phenotype dynamics are given by

$$x_1' = x_1(1+b)\exp\left(-\alpha\frac{x_1}{k} - \frac{e_{12}}{(1+d_1x_1)}\right),$$
$$x_2'(p) = x_2(p)\mathrm{e}^{-\sigma}E(p, e_{22}),$$
$$e = e(x), \tag{26}$$

where $E(p,q) = \Sigma_{i,j}\, p_i q_j \exp(c_2 E_{ij})$, $e_{12}(\xi_2)$ is the total predator population weighted mean of c_1, $\int c_1(p_1,\pi_2)\,\xi_2(\pi_2)\mathrm{d}\pi_2$, and $e_{22}(\xi_2)$ is the mean predator population strategy $\int p_2\xi_2(p_2)\mathrm{d}p_2/\int\xi_2(p_2)\mathrm{d}p_2$. We discretize these as as follows, denoting $x_2(p^l)$ by x_2^l and $c_1(p^l)$ by c_1^l,

$$x_1' = x_1(1+b)\exp\left(-\alpha\frac{x_1}{k} - \frac{e_{12}}{(1+d_1x_1)}\right),$$
$$(x_2^l)' = x_2^l e^{-\sigma}E(p^l, e_{22}),$$
$$e_{12} = \sum_l c_1^l x_2^l,$$
$$e_{22} = \sum_l p^l x_2^l / \sum_l x_2^l.$$

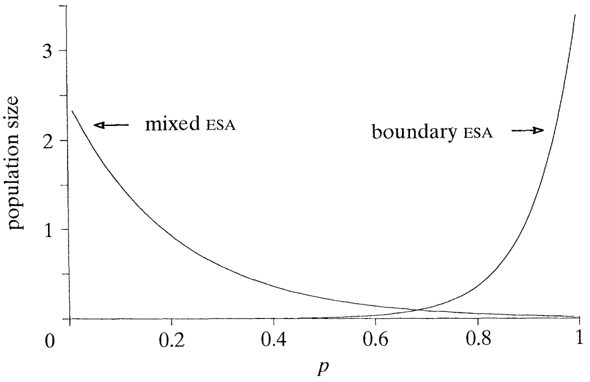

Figure 10. The asymptotic distributions for the phenotype dynamics for the Hawk–Dove predator–prey system. The value of the parameter C is 75.

Note that $c_1^t = c_1$ does not depend upon t since we assume that c_1 is the same for both Hawks and Doves. Therefore e_{12} is c_1 times the total predator population size.

Recall that this system has two ESA values separated by an evolutionary repellor at $p_r \approx 0.8$ (with quasi-periodic dynamics): the first at $p_* = V_0\bar{x}_1/C \approx 0.2 < p_r$ and the other a boundary ESA at $p = 1$. The phenotype dynamics reflects this. If the initial condition is a distribution with only phenotypes p with values greater than the evolutionary repellor p_r then, under the dynamics without mutation, it converges to a delta function at the boundary ESA. With mutation this asymptotic distribution is smoothed out. Other initial conditions converge to the distribution shown in figure 10 whose mean is at the interior ESA. This is not close to the delta function at p_* that might be naively expected, and the addition of mutation makes virtually no difference. The mean of this distribution is the ESA value, $p_* = V_0\bar{x}_1/C$. Thus, the population plays the same mean strategy as the pure ESA, but there is very great phenotypic variation in the population.

In figure 11 we show the time dependence of the mean strategy for two initial conditions which converge to each of the two asymptotic distributions.

This particular example is relatively easy to analyse. Note that the predator population mean strategy e_{22} is a function of the prey population size x_1 and the predator phenotype distribution x_2 and that x_2 only enters through the frequency of each predator phenotype p_2. Thus, we write $e_{22} = e_{22}(x_1,x_2)$. Let x_1^t and x_2^t denote respectively they prey population size and the predator distribution at time t. If, for all p_2, x_1^t and x_2^t are bounded away from 0 and ∞ uniformly in t as $t \rightarrow \infty$, then it follows that as $c_2 \rightarrow 0$, $e_{22}(\bar{x}_1,\bar{x}_2)$ is an ESS of the classical game where the prey population is fixed at its long time average $\bar{x}_1$. Here $\bar{x}_2$ is the long time average of the predator distribution x_2. Using this one can show that, as $c_2 \rightarrow 0$, (i) x_1^t and x_2^t are bounded away from 0 and ∞ uniformly in t if and only if $e_{22}(\bar{x}_1,\bar{x}_2)$ is an ESS of the classical game and (ii) in this case, the predator mean strategy converges to this ESS value. Moreover, note that if the mean strategy $e_{22}(\bar{x}_1,\bar{x}_2)$ is an ESS of the classical game, then $E(p,e_{22})$ does not depend upon p. Thus there is no selection on p. This is the reason why one gets non-trivial dispersed distributions (with mean the classical ESS) for such examples.

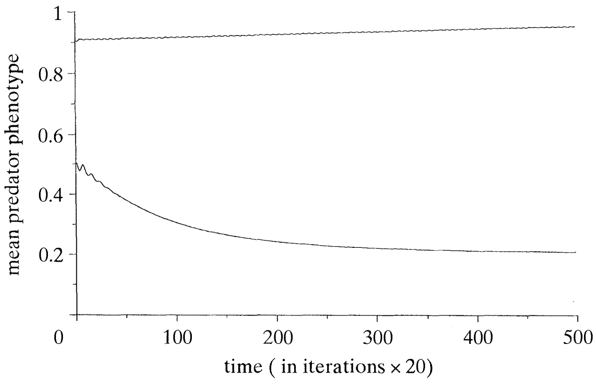

Figure 11. Time dependence of the mean strategy showing convergence to the two ESA values.

(ii) *Polymorphic populations*

The dynamical behaviour of polymorphic populations is very different. In a polymorphic population each individual plays one of the pure strategies and not a mixed strategy as in the previous case. Firstly, let us consider the pure equations for this system. The phenotype p of the predators belongs to the discrete set $P = \{H,D\}$. Those individuals with $p = H$ play the pure Hawk strategy and those with $p = D$ play the pure Dove strategy. The pure equations are given by

$$x_1' = x_1(1+b)\exp\left(-\alpha\frac{x_1}{k} - \frac{e_{12}}{(1+d_1x_1)}\right),$$

$$x_2' = x_2e^{-\sigma}E(p,e_{22}),$$

$$e_{12} = \text{predator population mean of } c_1 = c_1x_2,$$

$$e_{22} = \text{mean population strategy} = p. \qquad (27)$$

The notion of an ESA for the pure dynamics is not so interesting for this system because of the discreteness of P. Trivially the only possible ESAs correspond to systems that consist only of Hawks or only of Doves and small phenotypic mutations are not possible.

However, the phenotype dynamics which are obtained from this system are very interesting and are a generalization of the Jonker–Taylor–Zeeman dyna-

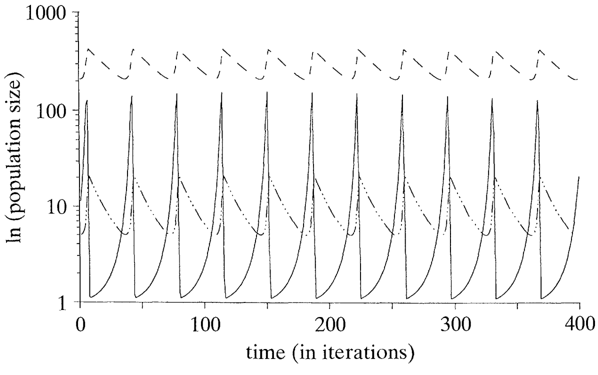

Figure 12. Time dependence of the numbers of Hawk and Dove predators and prey. Solid line, prey; dot-dashed line, Hawks; dashed line, Doves.

Table 6. *Parameter values for the Hawk–Dove predator-prey equation (28)*

b	c_1	c_2	d	k	V_0	C	σ
6.5	0.01	0.001	0.005	2000	1	450	0.006

mics (Taylor & Jonker 1987; Zeeman 1979). The equations for this are

$$x_1' = x_1(1+b)\exp\left(-\frac{x_1}{k} - \frac{e_{12}}{(1+dx_1)}\right) + 1,$$

$$\frac{x(H)'}{x(H)} = e^{-\sigma}\left(e_{22}^1\exp(c_2E_{HH}) + e_{22}^2\exp(c_2E_{HD})\right),$$

$$\frac{x(D)'}{x(D)} = e^{-\sigma}\left(e_{22}^1\exp(c_2E_{DH}) + e_{22}^2\exp(c_2E_{DD})\right),$$

$$e = e(x), \tag{28}$$

where $e_{22} = (e_{22}^1, e_{22}^2)$ is the mean predator population strategy and e_{12} is the predator population mean $c_1(D)x(D) + c_1(H)x(H)$ of c_1. The latter equals $c_1(x(D) + x(H))$ since we take $c_1(D) = c_1(H) = c_1$. The term 1 which is added to the right-hand side of the first equation represents a very small import of prey into the system. It is added to control numerical instability associated with near-extinctions. It does not affect our conclusions. Obviously, $e_{22}^1 = \pi(H)$ and $e_{22}^2 = \pi(D)$ where $\pi(H) = x(H) = x(H)/(x(H) + x(D))$ and $\pi(D) = 1 - \pi(H)$. The relation with the Jonker–Taylor–Zeeman dynamics should be clear to the reader from this.

When the prey are not present and the value of the resource is set at a constant V, then, as is well-known, any initial condition $(x(D), x(H))$ with $x(H) \neq 0$ and $x(D) \neq 0$ converges to $x(H) = V/C$ if $V/C < 1$ and to $x(H) = 1$ if $V/C > 1$. The behaviour is very different when the prey are present. For the parameter values in table 6, we observe complex oscillatory behaviour as shown in figure 12. For other nearby parameter values complex oscillatory patterns are observed.

Table 7. *Parameter values for the strategic prey equation (29)*

r	c_1	c_2	d_2	k	m
1.8	0.01	0.001	0.1	130	0.001

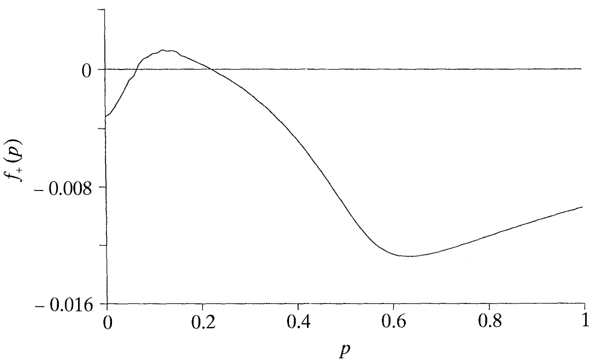

Figure 13. The graph of f_+ for the risk trade-off model (29) for parameter values given in table 7.

(*e*) *Phenotype dynamics for the predator–prey system with strategic prey*

We now consider another type of interesting phenotypic dynamics and introduce a new system. This is again a predator–prey system, but now we assume that the prey are strategic. Their strategy is represented by a number p in the unit interval $P = [0,1]$ which represents the weight given to searching for food. Those with $p = 0$ put a large effort into actively searching for food with a consequently higher risk of predation. Those with $p = 1$ do not actively search for food and are therefore immune to predation but likely to go hungry. Intermediate strategies are represented by intermediate values of p. For the pure equations and interactions we take the following:

$$x_1' = x_1(1+r)$$

$$\times \exp\left(-\frac{e_{11}^1}{k} - (1-p)\frac{c_1x_2}{(1+me_{11}^2)}\right) + \frac{x_1}{e_{11}^2}, \tag{29}$$

$$x_2' = x_2(1-d_2)\exp(e_{21}) + 1,$$

where $e_{11} = (e_{11}^1, e_{11}^2)$ is the pair consisting of the prey population weighted mean strategy and the total prey numbers and e_{21} is the prey population weighted mean of c_2. For the pure case, $e_{11}^1 = px_1$ and $e_{11}^2 = x_1$. As in the previous example, the terms x_1/e_{11}^2 and 1 are introduced to control numerical instabilities that arise because of near extinctions in the dynamics. The first term is chosen so that it goes to zero with x_1 to allow competition with successfully invading mutants to wipe the original population out. Normally, we would introduce a further interaction term corresponding to the total number of predators. However, as we are not going to consider mutations of the predator, this is not necessary.

In figure 13 we plot the graph of f_+ for this equation when the parameter values are as in table 7. We observe that there are two ESA values separated by an evolutionary repellor. There is a boundary ESA at $p = p_b = 0$ and evolutionary repellor at $p_r \approx 0.07$ and an ESA at $p* \approx 0.23$. In the phenotype dynamics these ESAs compete with the result that the mean strategy $\bar{p}$ oscillates in an irregular fashion between $p = 0$ and $p = 1$. When the system is near the state where $\bar{p}$ is close to 0 or 1, then the population's phenotypic distribution is bunched up close to this end-point. As the system moves to the opposite extreme all the individuals move to the other end of phenotype space. For this reason, and because the strategy is akin to confidence, we regard this as a biological business cycle.

6. LEARNING DYNAMICS

In this section we are interested in the following learning problem. We consider a general dynamical system of the form

$$\xi' = \Xi(\xi, x, c),$$

$$x' = \lambda(\xi, x, c).$$

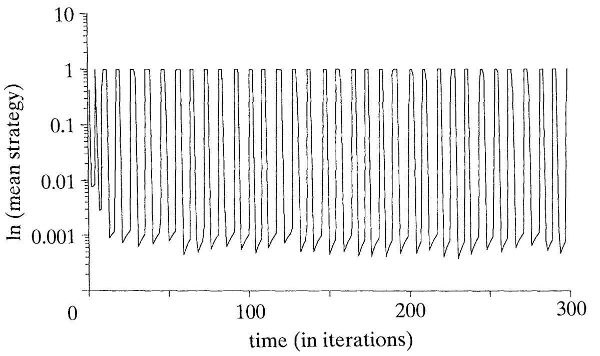

Figure 14. Time dependence of the mean prey strategy caused by the oscillating evolution between the two almost-boundary strategies.

Here ξ is some dynamically varying background environmental variable and x describes a distribution of strategies or behaviour amongst a population of agents. The variable c represents external control variables. Unlike our previous systems, the strategy dynamics are not given by reproduction but rather by learning. This is represented by the function λ which gives the learning rule. These can represent a sort of phenotype dynamics because x can contain distributions of strategies.

The function λ will be our phenotype and we will allow mutations in this learning rule.

As an example we will consider the following simple learning system. We assume a discrete set of strategies $S = \{1,. . ., m\}$ and assume a population Π consisting of individuals π. The state of the system is given by the configuration $\underline{\sigma} = (\sigma_{i,\pi})$ where $\sigma_{i,\pi}$ is the probability that $\pi \in \Pi$ plays strategy i.

We denote by $P_i(\underline{\sigma})$ the payoff to strategy i if the population is playing the configuration $\underline{\sigma} = (\sigma_{i,\pi})$. Then we define $\underline{\sigma}' = \lambda(\underline{\sigma})$ by

$$\sigma'_{i,\pi} = r_i + \frac{1}{Z}((\sigma_{i,\pi} - r_i)^m \exp(P_i(\underline{\sigma}) - \bar{P}(\underline{\sigma}))), \qquad (30)$$

where $\bar{P}(\underline{\sigma})$ is the population's mean payoff and Z is chosen so that $\Sigma_i\, \sigma'_{i,\pi} = 1$. Note that this generates the sequence

$$\sigma_{i,f}(t+1) = \frac{1}{Z}(r_i + \exp(m\tilde{P}_i(t) + m^2\tilde{P}_i(t-1) + \ \ldots\ )),$$

where $\tilde{P}_i(t) = P_i(t) - \bar{P}(t)$ is the excess payoff at the tth time step. This is analogous to the Harley learning rule (Harley 1981). The parameter m is a discount factor. It is also important to note that the initial condition $\sigma_{i,\pi}$ must satisfy $\sigma_{i,\pi} > r_i$. Otherwise the probabilities will become negative.

To make things simple let us further suppose that the payoffs are given in the usual linear way by a payoff matrix $E = (E_{ij})$. Then the payoff is given by

$$P_i(\underline{\sigma}) = \sum_j q_j E_{ij},$$

where $q_j = \Sigma_{\pi'}\sigma_{j,\pi'}/\Sigma_i\Sigma_{\pi'}\sigma_{i,\pi'}$ is the population's mean strategy.

The simplest case to consider is where $\Pi = \{1\}$. One can regard this as the situation where everyone is forced to play the same strategy. Then the state of the system is given by $\underline{\sigma} = (\sigma_i)$. It follows that $q_j = \sigma_j$.

We use the payoff matrix of our previous Hawk–Dove predator–prey system discussed in § 5*d*. Instead of being prey we regard the agents corresponding to the population $\xi = x_1$ as consumers and the agents corresponding to the predators as agents who either adopt a high-risk aggressive selling strategy (Hawks) or else are risk-averting (Doves). The strategic learning process λ is as described above.

Thus, if we let ξ denote the number of consumers, $x(D)$ and $x(H)$ denote the numbers of Hawk and Dove agents, $\tau = x(H) + x(D)$, $h = x(H)/\tau$, $d = x(D)/\tau$ and $\sigma = x(H)/\tau$, then our pure dynamics are given explicitely by

$$\xi' = \xi(1+b)\exp\left(- \frac{\xi}{k} - c_1\frac{\tau}{1 + d_1\xi}\right),$$

$$h' = r_H + \frac{1}{Z}(h - r_H)^m \exp(E(H,p) - E(p,p)),$$

$$d' = r_D + \frac{1}{Z}(d - r_D)^m \exp(E(D,p) - E(p,p)),$$

$$\tau' = \exp(c_3E(p,p)). \qquad (31)$$

The parameters are given in table 8. For these parameter values, the attractor of this system is a fixed point.

Now recall that we think of λ as the phenotype p and consider evolutionary stability to mutated learn-

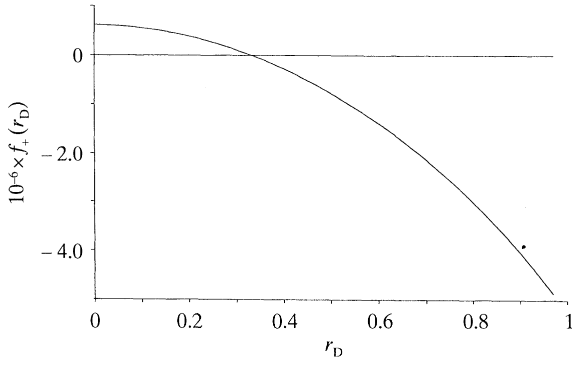

Figure 15. The graph of f_+ for the learning system given by equation (31) when $p = r_D$, for the parameter values given in table 8. The parameter r_H is set to 0.

Table 8. *Parameter values for the learning system given by equation (31)*

b	c_1	c_2	d	k	V_0	C	σ	c_3	m
0.5	0.01	0.001	0.001	1000	1	180	0.02	0.05	0.8

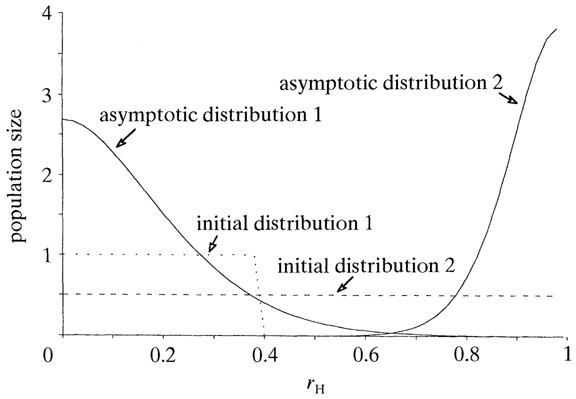

Figure 16. The asymptotic phenotype distributions for $p = r_H$ for the learning system given by equation (31). The parameter r_D is set to 0. With the distributions we show two initial conditions that converge to them.

ing processes. Here we only consider evolution within the class of learning processes λ of the form described above. These are parameterised by the discount factor m and the residual biases or preferences r_H and r_D. The evolution of m is simple. Under evolution, the value of m increases. Here we fix its value at 0.8.

Thus we consider $p = (r_H, r_D)$, for simplicity we consider these separately. Recall that we must have $r_i < 1$ since, as was pointed out above the initial condition $\sigma_{i,\pi}$ must be greater than r_i. For the Hawk's residual preference r_H there are two boundary ESAs at $r_H = 0$ and $r_H = 1$ separated by an evolutionary repeller. The value $r_H = 1$ is not a boundary ESA value in the usual sense. This is because in practise it cannot be realised because of the constraint $\sigma_{H,\pi} > r_H$. However, the system will evolve to values arbitrarily close to $r_H = 1$ if the initial strategy has a greater value than the evolutionary repeller.

For the Dove's residual preference r_D there is an interesting ESA at $r_D = r_D^* \approx 0.34$. The graph of f_+ for r_D is shown in figure 15. Thus we see that the learning evolves to give us a specific learning structure with a specific residual preference. We observed that the ESA value and the evolutionary repeller are given by a condition analogous to that for the classical linear Hawk–Dove game. They are precisely the values for which the proportion of time playing Hawk equals $\bar{V}/C$ where $\bar{V}$ is the mean resource value $V_0\bar{\xi}$.

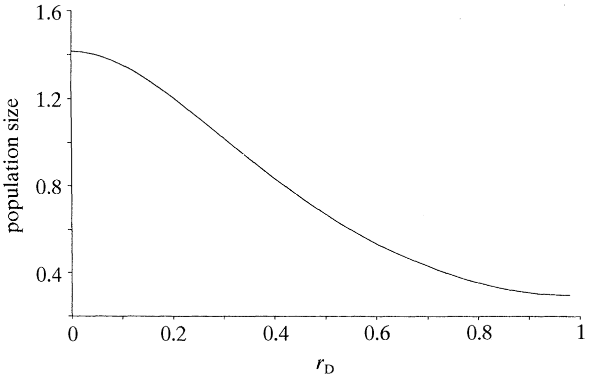

Figure 17. The asymptotic phenotype distribution for $p = r_D$ for the learning system given by equation (31). The parameter r_H is set to 0.

We then consider the phenotype dynamics for this system where we separately take the phenotype p to be one of r_H and r_D. We take the usual mutation process given by equation (24) in our phenotype dynamics. For $p = r_H$ initial distributions converge under the phenotype dynamics to one of two distributions depending upon initial conditions. These are shown in figure 16. They show great phenotypic variation. However, we believe that this is due to the fact that the selective pressures are small and therefore the effect of the mutation process is amplified. Without mutations, the system will converge to a delta function at one of the ESAs. For $p = r_D$ they converge to the interesting distribution shown in figure 17. This gives a wide distribution of phenotypes with mean value at the ESA value r_D^*. Thus we conclude that in such a population with phenotypic variation, the learning rule will evolve (under nonreproductive learning evolution) to one with the r_H having a very low or high value and the r_D having great phenotypic diversity around the mean given by the ESA value.

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APPENDIX 1. CONTINUOUS TIME AND ODES

In this appendix we very briefly discuss the modifications that are necessary when one is dealing with systems that are described by ordinary differential equations.

(i) *Mathematical formalism*

The general abstract form of the equations defining the pure dynamics analogous to equation (5) is then

$$\mathrm{d}x_i/\mathrm{d}t = X_i(x, e_i, p) \qquad (i = 1, \ldots, s),$$

$$e_i = e_i(x\delta_p; p_i). \tag{32}$$

The interaction parameters $e = (e_{ij})$ are defined as before. Thus each e_{ij} associates to any phenotypic distribution ξ_j a number or vector $e_{ij}(\xi_j; p_i)$.

Then the p'-mutated system is given by

$$\mathrm{d}x_i/\mathrm{d}t = X_i(x, e_i, p) \qquad (i = 1, \ldots, s),$$

$$\mathrm{d}y_i/\mathrm{d}t = X_i'(y, e_i', p') \qquad (i \in M),$$

$$e_i = (e_{ij}(x_j\delta_{p_j} + y_j\delta_{p_j'}; p_i))_{j=1,\ldots,s},$$

$$e_i' = (e_{ij}(x_j\delta_{p_j} + y_j\delta_{p_j'}; p_i'))_{j=1,\ldots,s}, \tag{33}$$

where M is the set of i such that $p_i' \neq p_i$. As before, we express the equation like this because we do not want to consider mutants which are the same as the original species.

To illustrate this consider our above resource–predator–prey system given by equation (3). An analogous continuous time system would be given by

$$\frac{1}{x_1}\frac{\mathrm{d}x_1}{\mathrm{d}t} = b_1 - \alpha\frac{e_{11}}{e_{13}} - \frac{e_{12}}{1 + d_1 e_{11}},$$

$$\frac{1}{x_2}\frac{\mathrm{d}x_2}{\mathrm{d}t} = -d_2 + e_{21},$$

$$\frac{1}{x_3}\frac{\mathrm{d}x_3}{\mathrm{d}t} = b_3 - \frac{e_{33}}{k} - e_{31}, \tag{34}$$

e_{ij} = population size of species group j (ij = 11, 13 and 33),

e_{ij} = species j population weighted mean of c_i (ij = 12, 21 and 31).

(ii) *Evolutionary stability*

The definition of evolutionary stability of an attractor is the same as in the discrete time case.

(iii) *Invasion exponent*

The variational mapping V is replaced by the following variational equation:

$$\mathrm{d}x_i/\mathrm{d}t = X_i(x, e_i, p) \qquad (i = 1, \ldots, s),$$

$$\mathrm{d}y_i/\mathrm{d}t = dX_i'(0, e_i', p') \cdot y_i \qquad (i = 1, \ldots, s),$$

$$e_i = (e_{ij}(x\delta_{p_j}; p_i))_{j=1,\ldots,s},$$

$$e_i' = (e_{ij}(x\delta_{pj}; p_i'))_{j=1,\ldots,s}. \tag{35}$$

Let V^t denote the flow associated to this. That is, if the initial condition is (x,y), then the state at time t is $V^t(x,y)$. We define the linear mapping T_x^t to be that such that $T_x^t \cdot y$ is the y-component of $V^t(x,y)$. To define the invasion exponent, we replace our discrete time definition of χ by

$$\chi(x) = \chi(x, p') = \liminf_{t\to\infty} \frac{1}{t} \log\|T_x^t\|, \tag{36}$$

and proceed as in the discrete time case.

As for discrete-time systems, we assume that, if $y_i = 0$ then $\mathrm{d}y_i/\mathrm{d}t = 0$. Then with this hypothesis and notation the results of § 4 carry over to continuous time systems after obvious modifications.

(iv) *Lotka–Volterra systems*

In our formalism the pure equation for Lotka–Volterra systems is given by

$$\frac{1}{x_i}\frac{\mathrm{d}x_i}{\mathrm{d}t} = r_i - \sum_{j=1}^{d} a_{ij}\, e_{ij} \qquad (i = 1, \ldots, d). \tag{37}$$

where $e_{ij}(\xi_j)$ is of the form $\int\alpha(p_j)\xi_j(p_j)\mathrm{d}p_j$ where $\alpha(p_j)$ is any smooth function of p_j. Thus e_{ij} could be total population size or biomass of the jth species group.

Obvious analogous results corresponding to each of those for the discrete case are true.

(v) *Phenotype dynamics*

The (mutation-free) phenotype dynamics are then given by

$$\frac{\mathrm{d}x_i(p_i)}{\mathrm{d}t} = X_i(x(p), e_i, p),$$

$$e_i = e_i(x; p_i), \tag{38}$$

where $x(p) = (x_1(p_1), \ldots, x_s(p_s))$, $p = (p_1, \ldots, p_s)$ and $e(x)$ is the value of the interactions corresponding to the distribution given by x.

APPENDIX 2. LEMMA 1, AGE-STRUCTURED POPULATIONS AND THE NON-GENERICITY OF STRONG STABILITY FOR CHAOTIC ATTRACTORS

(i) *Lemma 1*

We firstly prove lemma 1. Let $x_i = (x_{i,j})$ where $x_{i,j}$ denotes the number of individuals of age j where

$0 \leqslant j \leqslant l-1$. Then we assume that the age groups are linked by equations of the form

$$x'_{i,j+1} = x_{i,j}\phi_j(x,y) \qquad \text{for} \qquad j = 1, \ldots l-1,$$

$$x'_{i,0} = \sum_{j=1}^{l-1} x_{i,j}\psi_j(x,y),$$

where ϕ_j and ψ_j are positive. In this case the pure equations are given by

$$x'_i = A_i(x) \cdot x_i,$$

where $A_i(x)$ is a matrix of the form

$$A_i(x) = A_i(x,p) = \begin{bmatrix} a_0 & a_1 & \ldots & \ldots & a_{l-1} \\ b_0 & 0 & 0 & \ldots & 0 \\ 0 & b_1 & 0 & \ldots & 0 \\ \vdots & & & & \vdots \\ 0 & 0 & \ldots & b_{l-2} & 0 \end{bmatrix}.$$

The entries in the matrix are functions of x. Let $\bar{A}_i(x)$ denote the matrix of 0's and 1's obtained by replacing all non-zero entries of $A_i(x)$ by 1. Then we say that the age-structure if primitive if $\bar{A}_i = \bar{A}_i(x)$ is independent of x and there exists $n \geqslant 0$ such that the nth power of $\bar{A}_i$ has all its entries non-zero. In particular, this is the case if all the a_i and b_i are non-zero. We henceforth assume that the age-structure is primitive.

Suppose that x lies in the attractor Λ and that Λ is bounded away from 0 and infinity in the sense that there is $k > 0$ such that for all $x \in \Lambda$, $k^{-1} < x_{i,j} < k$.

If $x_i^n = (x_{i,j}^n)$ is the value of x_i after n iterates then $x_i^n = A_i^n(x) \cdot x_i$ where

$$A_i^n(x) = A_i(f^{n-1}x) \ldots A_i(x).$$

Since all the coordinates of x_i are positive, it follows from the bundle version of the Perron–Frobenius theorem that $\|x_i^n\|$ and $\|A_i^n(x)\|$ have the same growth rate. Since x^n is in Λ and therefore bounded away from 0 and ∞,

$$\lim_{n\to\infty} \frac{1}{n} \log\|A^n(x)\| = 0.$$

Now consider p' near p. Then $T_{x,i} \to A_i(x,p)$ as $p' \to p$. Thus

$$\chi_p(x,p) = \lim_{p \to p'} \chi_p(x,p') = \lim_{n\to\infty} \frac{1}{n} \log\|A_i^n(x,p)\|.$$

This proves lemma 1.

(ii) *Non-genericity for chaotic attractors*

We now consider the non-genericity of strong evolutionary stability for chaotic attractors. We assume that each y_i is 1-dimensional. If $\psi(x)$ is a function of x, then we denote by $\bar{\psi}$ the averaged function

$$\bar{\psi}(x) = \limsup_{n\to\infty} \frac{1}{n} \sum_{j=0}^{n-1} \psi(f^j(x)).$$

We will show that evolutionary stability implies that

$$\overline{d_{p'}\theta_i}(x,p) = 0, \tag{39}$$

for all periodic points x of the pure dynamics f. This is an infinite number of conditions which will only hold in very exceptional circumstances.

By (16) and lemma 1,

$$\overline{\theta}_i(x,p') = \overline{d_{p'}\theta_i}(x,p) \cdot (p'-p) + \mathcal{O}(|p'-p|^2).$$

If $\overline{d_{p'}\theta_i}(x_0,p) \neq 0$ for some periodic point x_0, then there are p' arbitrarily close to p such that $\overline{d_{p'}\theta_i}(x_0,p) \cdot (p'-p) > 0$. We now indicate why this implies that Λ is not evolutionarily stable.

In this case the periodic point $z_0 = (x_0,0)$ of the p'-mutated dynamics g has an unstable manifold $W_g^u(z_0)$ which contains points (x,y) with $y > 0$.

It follows that $\Lambda_0 = \{(x,0) : x \in \Lambda\}$ is not an attractor of g at least in the strong sense that there is a neighbourhood U of Λ_0 such that $g(U) \subset U$ and

$$\Lambda_0 = \bigcap_{n\geqslant 0} \overline{g^n(U)}, \tag{40}$$

for the reason given in the next paragraph. Thus Λ is not evolutionarily stable in the strong sense.

Suppose that there is a U such that $g(U) \subset U$ and $\Lambda_0 \subset U$. Then $W_g^u(z_0)$ is contained in U for the following reason. If $(x,y) \in W_g^u(z_0)$ then $g^{-i}(x,y) \in U$ for large i. But $g(U) \subset U$. Thus $(x,y) = g^i(g^{-i}(x,y)) \in U$.

As $W_g^u(z_0)$ is contained in U and $g(W_g^u(z_0)) \subset W_g^u(z_0)$, $W_g^u(z_0) \subset \bigcap_{n\geqslant 0} g^n(U)$.

Thus $\bigcap_{n\geqslant 0} \overline{g^n(U)}$ contains points of the form (x,y) with $y > 0$ and therefore is not equal to Λ_0. Consequently, Λ_0 is not an attractor of the form (40).

Note added in proof (21 January 1994): The following recent paper discusses a number of issues which, although they are in a different context, are closely related to our theorem 1. Of particular interest is the main theorem of this paper which effectively implies our theorem 1.

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