

How Should We Define 'Fitness' for General Ecological Scenarios?

J.A.J. Metz, R.M. Nisbet and S.A.H. Geritz

Beginners in life history theory or evolutionary ecology seemingly face a variety of almost unrelated approaches. Yet the biomathematical literature of the last 10–20 years reflects the implicit acceptance of a common evolutionary framework, the core idea being that there exists a unique general fitness measure that concisely summarizes the overall time course of potential invasions by initially rare mutant phenotypes. Using such an invasion criterion to characterize fitness implicitly presupposes a scenario in which, during periods of clear evolutionary change, the rate of evolution is set primarily by the random occurrence (and initial establishment) of favourable mutations. Evolutionarily stable life history strategies (ESSs) may then be regarded as traps for the evolutionary random walk.

Three recent books^{1–3} and one survey paper⁴ provide a comprehensive introduction to the mathematical machinery for dealing with the population consequences of complicated life histories and/or ecological scenarios. Our aim here is to sketch the implied evolutionary framework in bare outline, with a minimum of technical detail yet with reference to nontrivial examples. In particular, we note that although there is no general sense in which evolution 'maximizes fitness', under various simplifying assumptions many of the special optimization criteria that can be found in the literature may be derived from invasibility considerations. Later in the article we elaborate a little on the theme of the evolutionary random walk, concentrating in particular on the nature of the 'evolutionary attractors'. We conclude with some remarks concerning alternative genetic scenarios, and possible wider applications of the formalism.

The simplest selection model

The simplest textbook model for selection in large populations relies

J.A.J. Metz and S.A.H. Geritz are at the Institute for Theoretical Biology, University of Leiden, Kaiserstraat 63, 2311 GP Leiden, The Netherlands; R.M. Nisbet is at the Dept of Biological Sciences, University of California, Santa Barbara, CA 93106, USA.

on a number of assumptions: one locus with two alleles (say a and A), no (further) mutations, random mating, non-overlapping generations, differential survival prior to reproduction ('viability') as the only selective force, and fully constant relative individual viabilities. Invasion by A into a population made up of aa homozygotes is possible if (and effectively only if) the viability of the heterozygote aA exceeds that of the resident homozygotes. Let the difference between the logarithms of the heterozygote and resident homozygote viabilities be denoted as $s_a(A)$. This 'selection coefficient' equals the initial relative growth rate of the mutant frequency, after the initial hurdle of potential random extinction has been overcome. An aa population can be invaded by an A mutant if (and again effectively only if) $s_a(A)$ is positive.

We can immediately extend this result to temporally variable environments that affect only the viabilities, whether cyclical, random or chaotic, provided we define $s_a(A)$ to be the time average of the previously defined stepwise selection coefficients, which now take a different value at each time step. Provided there are no longlasting environmental trends, this time average is independent of the starting moment, or the replicate (if we are dealing with stochastic environments). Then the selection coefficient can be interpreted as the difference between the long-run (logarithmic) growth rates of the invader and the resident population.

Population dynamics in variable environments

The foregoing observations can be extended in principle to more complicated ecological scenarios, the only proviso being that we may neglect the possibility of long-term (or preferential) interactions among individuals. The essential point is that the dynamics of an invader can be represented by linear equations, possibly with time-varying coefficients. In this section we discuss the rudiments of the theory of linear

population equations, concentrating on finite dimensional discrete time models. The extension to infinitely many dimensions and/or continuous time involves some care with definitions, replacement of the word 'matrix' with 'linear operator', a lot of hard mathematical work, but no new biological ideas.

Consider a population, the individual members of which may be found in a finite number of ' i -states' representing physiological differences (for example in age, size or nutritional status) and/or ' x -states' representing spatial location. The ' h -state' (meaning heterogeneity) of an individual is the combination of its i - and x -state. The population at time t is described by a vector $\mathbf{N}(t)$ which has for its components the densities of the individuals in each h -state. We can denote the total population size as $|\mathbf{N}(t)|$. What happens to an individual, whether it migrates, changes i -state, gives birth or dies, depends in a probabilistic manner on its own h -state and on the overall condition of the environment $\mathbf{E}(t)$, and on nothing else. Here $\mathbf{E}(t)$ is a vector with quantities like the temperature, predation pressure, etc. at the different localities as components.

Assume for the time being that \mathbf{E} is given independently, as in the case of fully density-independent population dynamics. In that case,

$$\mathbf{N}(t+1) = \mathbf{B}(\mathbf{E}(t)) \mathbf{N}(t) \quad (1)$$

with $\mathbf{B}(\mathbf{E}(t))$ a matrix whose elements depend on $\mathbf{E}(t)$, implying

$$\mathbf{N}(t) = \mathbf{B}(\mathbf{E}(t-1)) \mathbf{B}(\mathbf{E}(t-2)) \dots \mathbf{B}(\mathbf{E}(0)) \mathbf{N}(0) \quad (2)$$

Assume now that the environmental process shows no longlasting trend. The so-called multiplicative ergodic theorem tells us that under very general conditions⁵ the relative sizes of the components of \mathbf{N} eventually become independent of $\mathbf{N}(0)$. It also tells us that the long-run growth rate, which can be defined as the limiting value, as (time) T approaches infinity, of the quantity

$$T^{-1} \{ \ln |\mathbf{N}(T)| - \ln |\mathbf{N}(0)| \} \quad (3)$$

is a fixed number. This number, which we denote by s because of the

analogy with our previous definition of selection coefficient, is known as the *dominant Lyapunov exponent* of the matrix process $\mathbf{B}(E(t))$, $t = 0, 1, 2, \dots$. When the dominant Lyapunov exponent is negative the population goes extinct. When it is positive the population will grow asymptotically at a relative rate s , though possibly with a lot of fuzz around the overall exponential trend.

When the environment is constant the dominant Lyapunov exponent reduces to the logarithm of the dominant eigenvalue of the matrix \mathbf{B} . For varying environments it is rarely possible to find simple procedures for calculating s . Some biologically meaningful cases where explicit expressions have been found are reviewed by Tuljapurkar^{3,4}. Such results are of great value as pointers to possible general principles and as benchmarks for numerical work. But they represent a considerable mathematical achievement, and are only possible with very particular assumptions about the environmental variations.

Where exact calculations of the dominant Lyapunov exponent are impossible or intimidating, there are two ways forward. If the environmental variation is small, perturbation methods are available. These can be particularly instructive in disentangling the effect of various patterns of variation, as for example in the analysis of the factors involved in the evolution of iteroparity by Orzack and Tuljapurkar⁵. A second possibility is direct numerical evaluation from simulations of the population process. It may appear perverse to compute a quantity that purports to predict the long-term growth rate from simulations. Yet the theory plays a vital role, guaranteeing the existence of a unique long-term relative growth rate. It even provides an asymptotic probability distribution of the population size, thus permitting estimates of s , with confidence limits attached, without excessive computational effort².

Equations (1) and (2) represent only book-keeping operations and as such still apply when the environment is itself influenced by the population state (see Box 1). Of course, in that case the amount of

Box 1. Lyapunov exponents for density-dependent population dynamics

This box has two purposes: (a) to illustrate with an example the use of the matrix formalism in population models with density dependence, and (b) to contrast the use of Lyapunov exponents in the population dynamics formulation described in this paper with their more widely publicized use in chaos theory²⁷.

Imagine a cannibalistic population consisting of juveniles with density $N_j(t)$ and adults with density $N_a(t)$. Each year an adult produces r juveniles of which a fraction $p \exp(-bN_a)$ survive to become adults the following year. The adults now constitute part of the environment for juveniles. The matrix \mathbf{B} in Eqn (1) is then

$$\mathbf{B}(E(t)) = \begin{bmatrix} 0 & r \\ p \exp(-bE(t)) & q \end{bmatrix} \text{ with } E(t) = N_a(t)$$

A bounded orbit (approaching an equilibrium, a limit cycle or a chaotic attractor) is characterized *inter alia* by the fact that the dominant Lyapunov exponent of the infinite matrix sequence $\mathbf{B}(E(0)), \mathbf{B}(E(1)), \mathbf{B}(E(2)) \dots$ is zero.

The second use of Lyapunov exponents, and the one that occurs in studies of chaos, involves a different sequence of matrices, obtained by *linearization* about a bounded orbit $\tilde{N}(0), \tilde{N}(1), \tilde{N}(2) \dots$. If we define $\mathbf{M}(t) = \mathbf{N}(t) - \tilde{N}(t)$, then to first order of approximation:

$$\mathbf{M}(t+1) = \mathbf{D}(t)\mathbf{M}(t)$$

with
$$\mathbf{D}(t) = \begin{bmatrix} 0 & r \\ p \exp(-b\tilde{N}_a(t)) & -bp \exp(-b\tilde{N}_a(t))\tilde{N}_j(t)+q \end{bmatrix}$$

The Lyapunov exponents of the infinite matrix sequence $\mathbf{D}(0), \mathbf{D}(1), \mathbf{D}(2) \dots$ characterize the *stability* of the orbit; in particular for the orbit to be considered chaotic, at least one of these exponents should be positive.

information that can be extracted from them is considerably less. However, they have one important consequence that we need for later use. When neither the variations in the environment nor those in the population state show longlasting trends, as is for example the case when there is no external forcing and the population state moves on a chaotic attractor, the dominant Lyapunov exponent of the matrix process $\mathbf{B}(E(N,t))$, $t = 0, 1, 2, \dots$, equals zero.

We can call s 'the fitness of a (life history) phenotype in a given environment'. Clearly, s does not share all the properties of the fitnesses of elementary population genetics (for example, it would no longer be permissible to talk about 'frequency-dependent fitnesses' as the formal counterpart of phenotype-dependent influences of the environment \mathbf{E}); this simply is too strong a requirement. However, the pay-off is a sharpening of our understanding of the links between population genetics and evolutionary ecology.

Evolutionary ecology

To analyse the initial fate of an A mutant entering a population made up of aa individuals, we note that (i) initially the densities of AA homozygotes will be negligible relative to those of the aA heterozygotes, and (ii) the densities of the aA heterozygotes will in turn be negligible relative to those of the

aa homozygotes. Let the stationary environmental time series which would result from the presence of only aa homozygotes be denoted as \mathbf{E}_{aa} . As a result of (i) and (ii) the population of aA heterozygotes cannot but satisfy (to first order of approximation) a linear recurrence of the form

$$N_{aA}(t+1) = \mathbf{B}_{aA}(\mathbf{E}_{aa}(t)) N_{aA}(t) \quad (4)$$

All the conclusions put forward for the simplest selection model generalize if we choose for $s_a(A)$ the dominant Lyapunov exponent of the matrix sequence $\mathbf{B}_{aA}(\mathbf{E}_{aa}(t))$, $t = 0, 1, 2, \dots$. Except in very contrived cases, A will replace a if both $s_a(A) > 0$ and $s_a(a) < 0$. (Note that for any acceptable population model $s_a(a) = 0$; the seemingly different case of r -selection is considered below.) The previous considerations apply equally to the density- and frequency-dependent cases⁶, as well as to situations with complicated attractors of the population dynamics, and environmental forcing.

When there is no external forcing and the resident aa population may be considered to be at equilibrium, \mathbf{E}_{aa} is constant, and $s_a(A)$ equals the logarithm of the dominant eigenvalue of the (now constant) matrix $\mathbf{B}_{aA}(\mathbf{E}_{aa})$. One immediate general result in this context is that, subject to the condition that lifetime offspring production increases with ambient food density, a stable population that is limited by a single food

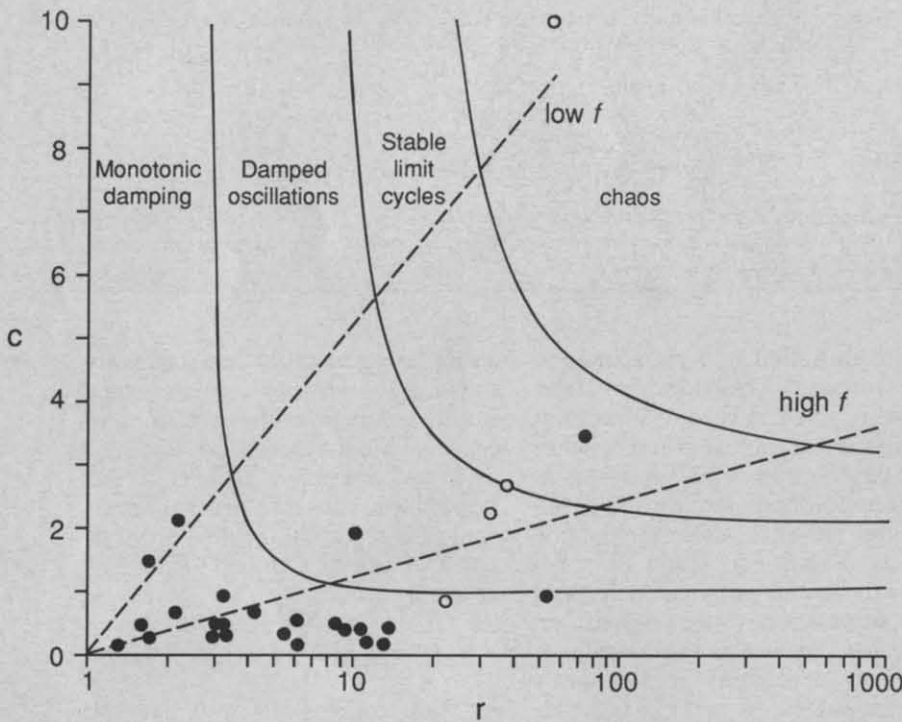
Box 2. The direction of evolution in an insect population model

The following example is adapted from Ref. 28. The figure below, taken from Hassell *et al.*²⁹, shows the distribution of parameters, as estimated by these authors from field (filled circles) and laboratory (open circles) data, of the discrete-time, unstructured, single-species population model

$$N(t+1) = B(N(t))N(t) \quad \text{with} \quad B(N(t)) = \frac{r}{[1+aN(t)]^c}$$

Also shown are the regions of parameter space corresponding to the different types of population behaviour (stable equilibria, cycles, or chaos). For *all* of these regions, if the population remains bounded, the dominant Lyapunov exponent of the sequence $\{B(N(t))\}$ will be zero, implying

$$s_0 = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} \ln B(N(t)) = 0 \quad (*)$$



To place the study of Hassell *et al.* in an evolutionary context, we interpret $N(t)$ as a component of the environment experienced by insects of generation t , and interpret r and c as properties of a particular genotype. We require to know whether a small population $N_i(t)$ of a mutant genotype can successfully invade the environment $N(t)$. For simplicity we consider a clonal model. The invader population initially obeys the linear equation

$$N_i(t+1) = B_i(N_i(t))N_i(t) \quad \text{with} \quad B_i(N_i(t)) = \frac{r_i}{[1+a_iN_i(t)]^{c_i}}$$

Whether invasion is possible depends on the Lyapunov exponent

$$s_i = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} \ln B_i(N_i(t))$$

which is the initial long-run growth rate of the invading mutant in the environment set by the resident genotype. With a little algebra, and use of equation (*), this expression reduces to

$$s_i = \ln r_i - (c_i/c) \ln r$$

which is positive if and only if

$$c_i^{-1} \ln r_i > c^{-1} \ln r$$

In other words, evolution will maximize the function $f(c,r) = c^{-1} \ln r$ to the extent that is physiologically feasible. Lines of constant f are shown (broken) in the figure (note that it is possible to achieve the same value of f in *any* dynamic regime). Evolution will tend to move a population from the top left to the lower right corner of the figure. Where evolution ends depends on the physiological trade-off between r , the reproductive capacity under favourable circumstances, and c^{-1} , a measure of the ability to cope with a bleak world.

resource can always be invaded by mutants able to persist at lower food densities.

We get the usual *r*-selection scenario if we assume that the environmental effects of the population state express themselves at any time step only as an equal proportional decrease of the survival probabilities of all players, independent of whether the population is decimated by rare catastrophes or is adjusted in a more continuous manner. In our framework, this is equivalent to the heterozygote dynamics allowing a representation of the form

$$N_{aA}(t+1) = B_{aA}(E_o, N_{aa}, t) N_{aA}(t) \\ = p(E_o, N_{aa}, t) Q_{aA}(E_o(t)) N_{aA}(t) \quad (5)$$

with an analogous equation for the resident homozygote dynamics (replace A everywhere with a). In this representation $p < 1$ is a scalar-valued function, and E_o stands for any external forcing of the environment like the weather. Q is a matrix whose elements depend only on E_o . From Eqn (5) it can be shown that $s_a(A)$ equals $r_{aA} - r_{aa}$ where r_{aA} and r_{aa} are respectively the dominant Lyapunov exponents of the matrix processes $Q_{aA}(E_o(t))$ and $Q_{aa}(E_o(t))$.

As yet, little work has been done on cycling or chaotic resident populations⁷⁻⁹ (M. Gatto, unpublished; R. Ferrière and J. Clobert, unpublished). However, Box 2 outlines the results of an invasibility calculation for a well-known model used previously to test for the occurrence of chaotic fluctuations in real populations.

The evolutionary random walk

If we assume that the speed of evolution is effectively mutation-limited, i.e. most mutations proceed to near-fixation before the next advantageous mutant enters the scene, we can picture evolution geometrically as the movement of a point X through some trait space. Here X is a vector whose components represent the values of the traits under study; successful mutations cause X to jump to a new value. The ecologically possible evolutionary paths can be described in the language of Lyapunov exponents: connected to any point X there is a set $H(X)$ of

points Y such that $s_x(Y) > 0$. Due to selection, a mutational step from X can only go to points in $H(X)$; thus the ecological contribution to evolutionary change is neatly summarized by the sign structure of $s_x(Y)$ considered as a function of the two variables X and Y .

Points X^* such that $s_x(Y) \leq 0$ for all (morpho)genetically possible $Y \neq X^*$ act as evolutionary traps. These are the evolutionarily stable strategies (ESSs)^{10,11}. At an ESS, the resident life history strategy maximizes fitness, measured by the dominant Lyapunov exponent, under the corresponding environmental conditions.

A problem with the ESS concept in its pure form is that even where an ESS exists there is no guarantee that the population will evolve towards it. A more stringent concept is that of a continuously stable strategy (CSS)¹²⁻¹⁴: an ESS X^* satisfying the additional requirement that $s_x(Y) > 0$ for all Y that in some sense lie 'between' X and X^* , for Y sufficiently close to X , and for all X sufficiently close to X^* . If mutations generally have small effect a CSS is surrounded by a basin of attraction in trait space.

A final consideration is that there may exist points X_0 in trait space which locally attract the evolutionary random walk, but which are not ESSs. Near such a point there exist mutually invisable points, so that the attraction towards X_0 spawns a polymorphism (Box 3), thus destroying our simple picture. Polymorphic situations are considerably more involved, and the overall theoretical picture is not entirely clear yet.

Concluding remarks

The take-home message is that the best available fitness measure in a variable nonlinear world is one based on dominant Lyapunov exponents. Reassuringly, many of the classical results in evolutionary genetics, in particular ESS considerations, generalize if we substitute these Lyapunov exponents for the selection coefficients. Less welcome is that obtaining explicit closed-form expressions is seldom possible. But the blow is softened by the fact that the theory enables us to interpret the results of simulations with added confidence.

Box 3. An example of a non-ESS evolutionary attractor

The following example is a special case of a class of models considered by van Tienderen and de Jong³⁰. Consider a population of haploid organisms, consisting of males and females. Assume that the fraction (x) of males among the offspring is determined solely by the genotype of the mother; as this is the only trait of interest in this particular model we can then specify genotypes by x . The organisms exploit resources which are divided into small discrete patches that are ephemeral in the sense that they persist for only two generations. Patches are colonized by one inseminated female each. The many offspring of these females mate within the patches and have offspring of their own. This second generation disperses to form a random mating pool before the next round of colonization starts.

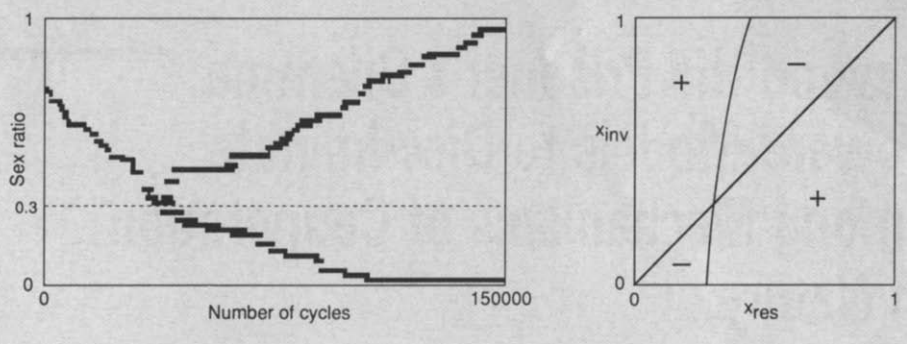
The relative frequencies (m_1, \dots, m_n), (f_1, \dots, f_n) of genotypes x_1, \dots, x_n among respectively the males and females during the dispersal phase can be related to the relative frequencies one cycle (of two generations) previously:

$$m'_i = \frac{\sum_{j=1}^n (3x_j + x_j)[(1-x_j)m_j f_j + (1-x_j)m_j f_j]}{\sum_{k=1}^n (3x_k - x_k)[(1-x_k)m_k f_k + (1-x_k)m_k f_k]}$$

$$f'_i = \frac{\sum_{j=1}^n (4-3x_j - x_j)[(1-x_j)m_j f_j + (1-x_j)m_j f_j]}{\sum_{k=1}^n (4-3x_k - x_k)[(1-x_k)m_k f_k + (1-x_k)m_k f_k]}, \quad i = 1, \dots, n$$

Simulation of this system, starting with a single sex-ratio genotype, and with nearby mutants being generated with a certain low probability per generation, shows that the population's sex ratio initially evolves towards an apparent attractor (left-hand figure below). However this attractor is not an ESS as the convergence is only transient; near the attractor, two separate branches develop and the population becomes dimorphic.

This phenomenon can be expressed in terms of the sign of the dominant Lyapunov exponent for a rare invader genotype x_{inv} in a background of some resident genotype x_{res} as shown in the right-hand figure. If only mutations of small effect occur, a population starting with an x -value below (resp. above) 0.3 will slowly drift upward (resp. downward). However a sex ratio of 0.3 is not evolutionarily stable since it can be invaded by all other sex ratios.



There are of course major problems as well. We have not discussed the effects of locally finite populations, thereby precluding dealing with any aspects of inclusive fitness^{15,16}. Throughout, we presuppose that evolution is effectively mutation-limited, i.e. can be treated as a sequence of single gene substitutions. Alternative paradigms exist, notably quantitative genetics¹⁷⁻²⁰, and it is far from clear whether a similar smooth extension to more general ecological scenarios can be made there. Luckily there exist some proofs that the usual ESSs also appear as 'final stops' for large classes of fairly complicated genetic architectures²¹⁻²⁵. We expect that these proofs can, with some effort, be extended to cover the kind of structured populations considered in this article, but only for the case of population

dynamical equilibrium. Whether analogous results hold good for fluctuating environments is an important, but probably extremely hard, open problem!

To end on a more positive note, although we have written this article with an eye on questions in evolutionary population ecology, the methods discussed are well established in studies of invasion and persistence in communities²⁶. Furthermore, mathematical methods relating to fitness and invasibility apply equally well to problems of 'unfitness' and extinction, notably those in conservation ecology, where the emphasis is on finding and controlling factors responsible for population decline⁴. Here environmental variability is again an issue, and theoreticians should (explicitly or implicitly) invoke Lyapunov exponents.

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Beyond the Prisoner's Dilemma: Toward Models to Discriminate among Mechanisms of Cooperation in Nature

Lee Alan Dugatkin, Michael Mesterton-Gibbons and Alasdair I. Houston

The iterated prisoner's dilemma game, or IPD, has now established itself as the orthodox paradigm for theoretical investigations of the evolution of cooperation; but its scope is restricted to reciprocity, which is only one of three categories of cooperation among unrelated individuals. Even within that category, a cooperative encounter has in general three phases, and the IPD has nothing to say about two of them. To distinguish among mechanisms of cooperation in nature, future theoretical work on the evolution of cooperation must distance itself from economics and develop games as a refinement of ethology's comparative approach.

Many of the theoretical frameworks used in modern behavioral

ecology have been imported from economics. A case in point is the study of the evolution of cooperative behavior: Hamilton¹ used economic optimization models to formalize inclusive fitness theory and its ramifications for the evolution of cooperation, while Trivers² suggested in his seminal paper that cooperation among unrelated individuals may best be studied using methods developed in economic game theory.

Lee Alan Dugatkin is at the Dept of Biology, Mount Allison University, Sackville, New Brunswick, Canada E0A 3C0 (from 1 July 1992: T.H. Morgan School of Biological Sciences, University of Kentucky, Lexington, KY 40506-0225, USA); Michael Mesterton-Gibbons is at the Dept of Mathematics B-154, Florida State University, Tallahassee, FL 32306, USA; Alasdair Houston is at the Dept of Zoology, University of Oxford, South Parks Road, Oxford, UK OX1 3PS.

A game is a mathematical model of conflict or bargaining. Game theory explicitly recognizes that an individual's fitness depends not only on its own behavior but also on the behavior of others. Economic game theory has failed to provide a model for every occasion, however, and in such circumstances behavioral ecologists have been remarkably resourceful in developing their own product. The most celebrated example is surely Maynard Smith's concept³ of evolutionarily stable strategy, or ESS, which economists have imported into their literature in recent years to complete a cycle of trade.

If the success of a model is measured by the size of the literature it spawns, then the most successful model in studying the evolution of cooperation is unquestionably the prisoner's dilemma, or PD. The PD is a two-player, two-strategy game with both pay-off and informational symmetry (see Box 1). In the PD, a player chooses either to cooperate (C) or to defect (D = not cooperate). On any single move of the game, to defect yields a greater pay-off than to cooperate (as $T > R$ and $P > S$), but mutual cooperation