On the Evolution of Behavioral Heterogeneity in Individuals and Populations

CARL T. BERGSTROM
Department of Biological Sciences

and

PETER GODFREY-SMITH
Department of Philosophy
Stanford University
Stanford, CA 94305, USA

Abstract. A wide range of ecological and evolutionary models predict variety in phenotype or behavior when a population is at equilibrium. This heterogeneity can be realized in different ways. For example, it can be realized through a complex population of individuals exhibiting different simple behaviors, or through a simple population of individuals exhibiting complex, varying behaviors. In some theoretical frameworks these different realizations are treated as equivalent, but natural selection distinguishes between these two alternatives in subtle ways. By investigating an increasingly complex series of models, from a simple fluctuating selection model up to a finite population hawk/dove game, we explore the selective pressures which discriminate between pure strategists, mixed at the population level, and individual mixed strategists. Our analysis reveals some important limitations to the "ESS" framework often employed to investigate the evolution of complex behavior.

Key words: game theory, ESS, mixed strategy, polymorphism, variation in behavior, finite populations

1. Introduction

A primary goal of many ecological and evolutionary models is to explain the maintenance of variety in behavior or phenotype in equilibrium populations. There are, however, several distinct ways in which variety can be realized in a population. The first, basic distinction is between *population-level* and *individual-level* variability. It may be that each individual has the capacity to produce a variety of behaviors – each individual may alternate between cautious and adventurous behaviors, for example. Alternately, the population may consist of different types of individuals, each having the capacity to produce only a single behavior. In the first case we have a simple population of complex individuals; in the second we have a complex population of simple individuals.

It has been quite common for optimality models which address questions about the evolution of variable behaviors to treat these possible states as equivalent. For example, Levins (1968) uses a decision-theoretic framework to investigate the conditions under which populations will respond to environmental variability with a mixture of behaviors rather than a single cover-all or a specialized behavior. Levins' model does not differentiate between genetic polymorphism and individual-level mixing of behaviors[1].

A similar blurring of this distinction is found in much of evolutionary game theory (Maynard Smith and Price 1973; Maynard Smith 1982). The original formulations of evolutionary game theory represent diversity in behavior with the concept of a "mixed strategy." The basic mathematical apparatus of evolutionary game theory does not differentiate between mixed strategies played by individuals – such as "behave aggressively with probability P" – and mixtures realized by polymorphic populations of individuals playing pure strategies. The original formulations of evolutionary game theory were not required to make this distinction, because they assume effectively infinite population size. In many examples of games in which a mixed strategy is predicted, such as the Hawk-Dove game, the theoretical apparatus finds a mixture of behaviors such that the expected payoffs for each behavior are the same. This mixture cannot be invaded by any other single strategy. Such a state can be realized either by each individual playing hawk with probability P and playing dove with probability $(1 - P)$, or it can be realized by a polymorphism in the population where each individual always plays the same "pure" strategy, and the proportion of the population which plays hawk is P. Under infinite population assumptions, these two cases cannot be distinguished by evolutionary game theory.

Thomas (1984) describes this type of model, which does not distinguish between different realizations of the evolutionarily stable state, as "degenerating." He contrasts these degenerating models with a "non-degenerating" class of models which predict not only the evolutionarily stable state but the evolutionarily stable strategy by which that state will be realized.[2] In this paper, we will be concerned with degenerating models only. While no single strategy can be uninvadable in a degenerating model with no pure strategy equilibria (Thomas 1984), in this paper we investigate the selective forces which may generally favor mixed strategists over pure strategists, or vice versa, in degenerating models.

One aim of this paper is to stress the importance of the *distinctions* between these different realizations of biological complexity and variability. If the game theoretic apparatus applied in degenerating models is not able to distinguish between complex populations of simple (pure strategist) individuals and simple populations of complex (mixed strategist) individuals, what should we

expect to find in nature? Under what conditions do these realizations of complexity have different evolutionary roles? In particular, under what conditions does natural selection discriminate between these alternatives?

In this paper we will discuss four different effects, arising in dynamic models, which do discriminate between different realizations of variability. Some of these factors have only local importance, while others are more general in their application. All of these effects have been described individually before, in some cases in detail and in other cases in a more cursory fashion. However, they have not previously been integrated in a single picture.

We will discuss a series of models of increasing complexity. The most complex case discussed will be a finite Hawk-Dove game, a two player contest over a resource. We will focus on this case in particular because, despite the simplicity of the game itself, when it is played in a finite population the different effects interact in complicated ways. One methodological point to which we wish to call attention is the superiority of dynamic methods over static ESS methods for investigating many of these questions. Methods which are designed to ask questions only about distributions of behaviors, and not about how these distributions are realized, will in many cases obscure the issues which are addressed in this paper. The dynamic methods, on the other hand, naturally attend to the distinctions between different realizations of variability.

As the paper is focused on differences between ways in which variability can be realized, we need terminology to mark these distinctions. We will use the term "mixed strategy" to refer only to mixtures which are realized in individuals. A mixed strategist is an individual with the capacity to produce a variety of behaviors. In the cases we examine here, mixed strategists produce these behaviors randomly rather than by tracking the state of the world with the aid of a cue.

Within the category of mixed strategists, we distinguish those cases in which each individual does different things on different occasions, and those cases in which an individual makes a single choice that determines all its behaviors over its lifetime. In this latter case it is as if a genotype is playing the mixed strategy; each individual of that genotype has the capacity for a variety of behaviors but exhibits only one. If each individual chooses a single behavior, this will be called *developmental coin-flipping*.[3] If each individual exhibits variety within its lifetime, this will be called *individual behavior mixing*. In this paper we shall be less concerned with this distinction than with that between mixed strategies and polymorphisms. However, one of the effects that we will discuss does distinguish between these two individual-level realizations of heterogeneity.

The terms "population-level mixture" and "polymorphism" will be used to denote the case where the population consists of individuals each of which can produce one behavior only, but where different individuals produce different behaviors. All the individuals of a given genotype exhibit the same fixed behavior. An evolutionarily stable polymorphism, which cannot be invaded by any single alternative strategy, is referred to as an evolutionarily stable state. This is in contrast to an evolutionarily stable strategy (ESS), a single (possibly mixed) strategy which cannot be invaded by any single (possibly mixed) alternative.[4] This not to say that an ESS cannot be invaded by some *combination* of alternative strategies.

We must also attend to the distinction between *behaviors* (such as "hawk") and *strategies* (such as "always play hawk"). Additionally, notice that variety in behavior can be expressed not only by monomorphic populations of mixed strategists and polymorphic populations of pure strategists, but also by polymorphisms of mixed strategists. Models involving these populations, treated by Schaffer (1988), will not be considered in this paper.

2. Replicator dynamics in a variable environment: the geometric mean fitness effect

The first model we discuss does not use game-theoretic concepts at all. It is intended as the simplest possible illustration of an effect which will play a role in all the models we will discuss – the advantage that mixed strategies gain from their reduced fluctuation in payoff across trials. The model is borrowed from discussions in Seger and Brockmann (1987) and Cooper and Kaplan (1982).

Consider an infinite population of asexual haploid organisms with non-overlapping generations, subject to natural selection. Each organism contributes progeny identical to itself to the next generation in proportion to its fitness during its lifetime; this selective scheme, termed *replicator dynamics*, functions as a basic model of evolution via natural selection. Mathematically, replicator dynamics are expressed by the following equations:

$$p_i(t+1) = \frac{p_i(t)w_i}{\bar{w}}, \qquad \bar{w} = \sum w_i p_i \tag{1}$$

The frequency of genotype i at time $t+1$ is equal to the frequency of genotype i at time t, times the ratio of the fitness of genotype i to the mean fitness $\bar{w}$. These fitnesses w_i may be constant, or may change from census point to census point.

In the model presented in this section, the environment is variable over time. Each individual lives for a season; there are wet seasons and dry seasons which occur with equal probability and with no correlation over time.

Table 1. Genotype fitnesses: wet-year fitness, dry-year fitness, and geometric mean of wet and dry-year fitness.

	A_1	A_2	A_3
Wet Year	1	0.6	0.7
Dry Year	0.5	1	0.875
Geom. Mean	.707	.775	.783

Suppose that there are three genotypes A_1, A_2, and A_3. Of these, A_1 is a wet-year specialist and A_2 is a dry-year specialist. These are genotypes for pure strategies, producing the same individual phenotype in all cases. A_3 is a developmental coin-flipping mixed strategist, producing the phenotype associated with A_1 with probability 0.25 and the phenotype associated with A_2 with probability 0.75. In any one year, some individuals of type A_3 will have the wet-year phenotype and some will have the dry-year phenotype. Borrowing the parameter values of Seger and Brockmann (1987), the relevant fitness properties of the three genotypes are given in Table 1.

Consider first the fitness relationships between A_1 and A_2. In each year either the wet-year or the dry-year specialist is favored. The average rate of increase of a genotype i across a series of years is measured by its geometric mean fitness. If wet and dry years occur with equal frequency in a particular series, the average fitness $\bar{w}_i$ of genotype i is given by the following expression.

$$\bar{w}_i = \sqrt{w_{i_{wet}} \times w_{i_{dry}}} \tag{2}$$

In this case A_2 has a higher geometric mean fitness than A_1. However, A_3 has a higher geometric mean fitness again.

The important role played by geometric mean fitness in circumstances where there is variation in payoff over time was first recognized by Dempster (1955) and Verner (1965). Geometric mean fitness is sensitive to fluctuation across trials; it is reduced, in comparison to an arithmetic mean, by such fluctuation. More detailed genetic models of this *geometric mean fitness effect* were developed by Haldane and Jayakar (1963), Gillespie (1973), Hartl and Cook (1973), Karlin and Lieberman (1974), and others.[5] A mixed strategy in circumstances of environmental fluctuation has a sort of "homeostatic" property: by means of the production of variable phenotype or behavior *within* a trial, fluctuation in fitness *across trials* is reduced, increasing geometric mean fitness. In the case above, this makes the mixed strategy superior to both specialists.[6]

Furthermore, in this model it is not possible for an equivalent result to be achieved through a polymorphism of A_1 and A_2. Suppose the population is in a polymorphic state with 25% A_1 and 75% A_2. This state mimics A_3 at the

population level, but such a polymorphism is not stable; A_2 will be fixed at the expense of A_1. Moreover, A_3 can invade any mixture of A_1 and A_2 and go to fixation.

2.1 Developmental coin-flipping vs. individual behavior mixing

The models of Cooper and Kaplan (1982) and Seger and Brockmann (1987), as well as the model above, consider the case of mixed strategy effected by the mechanism of developmental coin-flipping. In the dynamical system describing the change of genotype frequencies in the population, the fitness of a developmental coin-flipping gene (relative to the fitness of population at large) is the arithmetic mean of the fitnesses of the two behaviors which it plays in different individuals.

Alternatively, a genotype can express a mixed strategy through individual behavior mixing. Are the population-genetic dynamics of these methods of expression of the mixed strategy equivalent? The answer depends on how the fitness of an individual expressing both strategies is evaluated. If the fitness of such an individual behavior mixer is simply the frequency-weighted arithmetic mean of the fitnesses of the two pure strategies, the individual behavior mixing case will be equivalent to the developmental coin-flipping case in infinite population models. This is not always a fair assumption, however. If the mixed strategies are expressed sequentially within a generation, and if fitnesses in each stage represent survival probabilities, the geometric mean of the fitnesses of the two behaviors will be the appropriate metric of lifetime individual fitness. In other cases, an arithmetic mean is entirely appropriate. For example, the fitnesses from each stage may correspond to total acquired resources to be converted into offspring production, or the probability of achieving a mating with a female in a given interaction. In other cases still, the appropriate metric of lifetime fitness will be some more complex function.

In the remainder of this paper, we will generally discuss mixed strategies in the context of individual behavior mixing, making the assumption that arithmetic mean fitness is indeed the appropriate metric of lifetime fitness. The mathematical equations for the developmental coin-flipping case will be the same as those for the individual behavior mixing case in infinite population models. In finite population models, the developmental coin-flipping dynamics run across an integer problem, in that not all fractional strategies can be expressed in a population of a given size, and for this reason differ slightly from the individual behavior mixing examples treated here. Moreover, there is an additional difference, discussed in Section 4, between developmental coin-flipping and individual behavior mixing in games where individuals don't "play against themselves."

3. The oak/maple game in a finite population

In the first model discussed, the fluctuations in payoff experienced by individuals were a consequence of variability in the physical environment. The next case we will examine features frequency-dependent fitnesses; the payoffs associated with each behavior are dependent on the composition of the population itself. Fluctuations in the "environment" encountered by individual agents, and hence fluctuations in fitness over time, are a consequence of fluctuations in the composition of the population induced by the sampling properties inherent in the reproductive process.

3.1 The model

Consider a population of asexual haploid organisms that have available to them two alternative food sources, found in oak and maple trees respectively. A single gene determines which food source will be chosen. Although there are only two different food sources, there are three different genotypes determining three different strategies for food gathering. The first of these is to forage exclusively in oak trees (O), the second is to forage exclusively in maple trees (M) and the third is the mixed strategy (I) of foraging in oak trees half the time and maple trees half the time.[7]

The two foraging locations, oaks and maples, each have an equal share of the total resource $4c$, with $2c$ in oaks and $2c$ in maples. Individuals playing O share equally among themselves from the $2c$ in oaks, and likewise individuals playing M receive equal shares from the $2c$ in maples. Individuals playing the mixed strategy I each forage in each place half of the time, and hence receive a half-share from the oak allocation and a half-share from the maple allocation.

Suppose that there are no sampling effects. It should be clear that the payoffs associated with behaviors are equal when half of the foraging occurs in oaks and half of the foraging occurs in maples. Foraging in oaks is beneficial when more individuals are foraging in maples than in oaks, and vice versa.

At the level of strategies, there are various ways that a state with an equal number of oak and maple foragers can be realized. There could be a polymorphism of O and M, each at frequency of 0.5. Alternatively, the population could be monomorphic for I. Thirdly, the population could contain some portion of I and the remainder be equally divided between O and M. When an infinite population is at any one of these states, it is said to be in an evolutionarily stable state – with respect to *behaviors* – and all behaviors have equal payoffs.

3.2 Dynamic model of the oak/maple system: the basic mixed strategy advantage

In this section we will use the oak/maple game in a *finite* population to outline the second of the four effects discussed in this paper, the *basic mixed strategy advantage*. In a given generation, let o denote the fraction playing oak and m the fraction playing maple. Suppose that there are three haploid types, pure O players with frequency in the population of x_1, pure M players with a frequency of x_2, and mixed strategists I which mix the oak and maple behaviors equally with a frequency in the population of y. Let $\bar{w}$ be the mean fitness in the population. After a single generation, the expected frequencies of each haplotype are

$$\bar{w}x_1' = \frac{2x_1 c}{o}$$
$$\bar{w}x_2' = \frac{2x_2 c}{m} \tag{3}$$
$$\bar{w}y' = yc\left(\frac{1}{o} + \frac{1}{m}\right)$$

At this point, let $x_2 - x_1 = 2d$, where $2d$ is the fraction of M players minus the fraction of O players. Using the fact that $x_1 + x_2 + y = 1$, $o = y/2 + x_1$, $m = y/2 + x_2$, and $\bar{w} = 4c$, the equations above become

$$x_1' = \frac{(1 - 2d - y)}{2(1 - 2d)}$$
$$x_2' = \frac{(1 + 2d - y)}{2(1 + 2d)} \tag{4}$$
$$y' = \frac{y}{(1 - 4d^2)}$$

Now, let μ_t be the ratio of pure strategists to mixed strategists in generation t, i.e., $\mu_t = \frac{x_1 + x_2}{y} = \frac{1-y}{y}$. Applying the above equations for x_1', x_2', and y', algebra yields an equation for μ_{t+1} in terms of μ_t:

$$\mu_{t+1} = (x_1' + x_2')/y' = (1 - y - 4d^2)/y = \mu_t - 4d^2/y \tag{5}$$

Therefore, $\mu_{t+1} \leq \mu_t$, for all x_1, x_2, and y, the number of pure strategists is expected to be non-increasing. In a finite population, there will of course be fluctuation in frequency associated with the sampling process of reproduction; here, we describe merely the *direction* of selection. Moreover the pure

strategists are replaced by the mixed strategists at a rate proportional to the squared difference between the fractions of O and M players. At the very best, the pure strategists are able to hold their own but make no gains against the mixed strategists, when there are exactly as many pure O players as pure M players.

In this system, there is an inevitable advantage to the mixed strategist. Whenever the population is away from equilibrium with respect to behaviors, the fitness of I is always higher than the average fitness in the population. Consequently, the frequency of I is expected to increase whenever the population is away from the equilibrium ratio of behaviors.

This effect is a consequence of the basic mathematical properties of negative frequency dependence in fitness. The rare behavior is always favored. As a result, the *more common* pure strategist is always the *less fit* pure strategist. The mixed strategist does not do as well as the rare pure strategist, whichever one that is, but it is always doing better than the population average, when the system is away from the equilibrium mixture of behaviors. This we call the *basic mixed strategist advantage*. The first and most systematic discussions of this effect of which we are aware are presented by Hines (1980, 1987).

This effect plays a role in all of the models to follow, for each of these models will feature an advantage to rare behaviors. It does not play any role in the stochastic replicator dynamics model of Section 2, because in that model there is no advantage to rarity. The favored behavior in that model is the one for which the environment happens to be suitable; this could be either the common or the rare behavior.

It is important to recognize that this model shows the direction of selection, considered *deterministically*. Therefore its result states that at almost any point in the space of strategy frequencies, the direction of selection is such that mixed strategists are favored to replace pure strategists. Random fluctuations caused by the sampling inherent in the reproductive process may serve to alter strategy frequencies independently of this direction of selection. Notice that the model above does not explicitly treat this process of fluctuation – the difference between the number of pure O and pure M players is treated as a variable with unknown distribution over time. Instead, the model relies upon the fact that in a finite population, sampling error is inevitable and therefore d must sometimes be non-zero, in order to conclude that the mixed strategists are selected to replace the pure strategists.

Furthermore, this model does not take into account the "geometric mean fitness" effect discussed in Section 2. Since the present model examines the fitnesses at one instant in time, fluctuation in fitness across generations and consequently geometric mean fitnesses are beyond its scope. With the geometric mean fitness effect playing no role in this particular formulation of
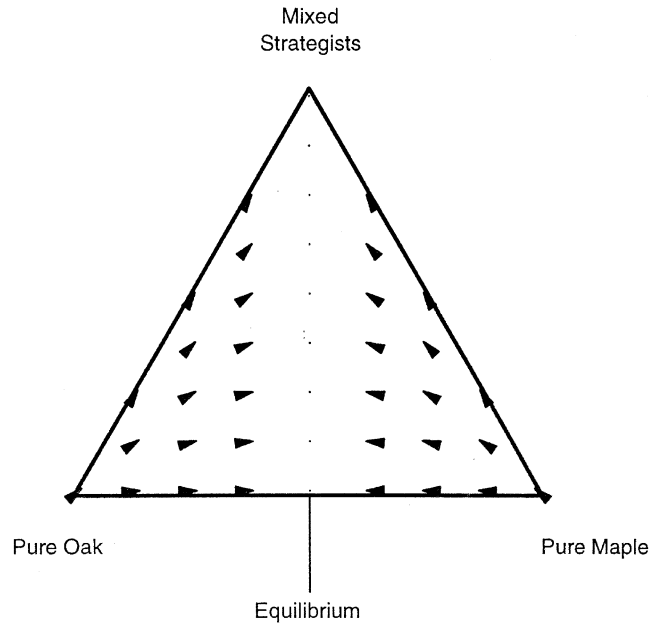
214

Figure 1. De Finetti diagram for the oak/maple game, for a population of size $n = 20$.

the model, it is clear that the deterministic "basic mixed strategist advantage" is a phenomenon distinct from the geometric mean fitness effect.

The results of this model can be seen in the diagram pictured in Figure 1. This diagram represents the direction of selection at each point on the simplex,[8] where each point represents a population composed of a different fraction of pure O, pure M, and mixed strategist I players. At the equilibrium ratio of Oak and Maple foragers, pure and mixed strategies are neutral toward each other, as evidenced by the column of zero vectors down the middle of the simplex. However, at all points away from the equilibrium ratio, the vectors point not horizontally as would be expected if pure and mixed strategists were neutral to one another, but diagonally upward, indicating that mixed strategists are favored away from equilibrium.

3.3 The Geometric Mean Fitness Effect

Though not represented in the model of Section 3.2, the geometric mean fitness effect will play a role in the oak/maple game as well. In the model of Section 2, strategies experienced fluctuations in fitness, and a mixed strategy was favored over pure strategies as a consequence of its reduced fluctuation in payoff and consequent higher geometric mean fitness. In that model, the

fluctuations in fitness were a consequence of variability in the physical environment. In the oak/maple game played in a finite population, strategies again experience fluctuations in fitness, in this case as a consequence of fluctuations in the composition of the population itself. These fluctuations are due to the sampling properties inherent in the reproductive process.

In the stochastic replicator dynamics case of Section 2, all three of the strategies can have good years and bad years. The mixed strategist has less successful good years, and less disastrous bad years, but it is possible for the mixed strategist to have a fitness which is lower than the population average in a particular year. This will happen when the favored pure strategist has a high frequency. Though all the strategies can have good years and bad years, in comparison to the rest of the population, the mixed strategist is favored because of its low fluctuation in fitness and consequently, its high geometric mean fitness. In the oak/maple game, on the other hand, there is never a year in which the mixed strategy has a lower fitness than the population mean. Its frequency is expected to increase *whenever* the population is away from the equilibrium distribution of behaviors, whatever the exact pattern of frequencies. However it is also the case that the mixed strategist's low fluctuation in fitness across years will give it some further advantages. The relation between generations is multiplicative, as before, so reduced fluctuation is advantageous.

Also, one should notice that there is a difference between the nature of the two effects. The basic mixed strategy advantage is *deterministic*. The argument asserts that a mixed strategy, at any point in frequency space, is expected to increase in frequency. This is shown in Figure 1. The geometric mean fitness argument, on the other hand, is *stochastic*. In an actual finite population, evolving over time, these two effects will act simultaneously. The mixed strategists will have higher fitness than the population average at any point in time when the population is away from the equilibrium distribution of behaviors, because of the basic mixed strategy advantage. Moreover, pure strategists will tend to have greater fluctuation in fitness than will the mixed strategists, resulting in a reduction of the pure strategists' fitness over a *series* of generations. In the next section, we consider one additional stochastic effect aiding the mixed strategists.

3.4 *The pure strategist co-dependence effect*

The *pure strategist co-dependence effect* is another stochastic effect which selects against pure strategists. The existence of this effect in a system of this type was noted by Vickery (1988). We will discuss it in an informal way here.

For the pure strategists to have a reasonable chance of surviving for any length of time in the population, both types of pure strategists, O and M, must be present in the population. Otherwise the single remaining type of pure strategist will always be foraging in the overused location and receiving lower payoffs than the mixed strategists. If either type of pure strategist is lost, the pure strategists as a class are very likely to be eliminated from the population.

Consider a population consisting of half mixed strategists, half pure strategists (one quarter O, one quarter M). It is much more likely that either all O or all M pure strategists will be lost than that all the mixed strategists will be lost, by simple sampling error of the reproductive process. Consider a "neutral" model where the pure and mixed strategists receive precisely the same payoffs, but loss of either pure type ensures fixation of the mixed strategists. In a population starting with half pure strategists (again one quarter O, one quarter M) and half mixed strategists, mixed strategists will eventually be fixed with $5/6$ probability.[9]

The oak/maple game is somewhat more complicated, in that a pure strategy, when rare relative to the other pure strategy, experiences a strong selective advantage and is likely to bounce back from near extinction, whereas the mixed strategy enjoys no such buffer against extinction.[10]

4. The anti-coordination team game

In this section, we will look at another deterministic effect which distinguishes between pure and mixed strategists. This effect, unlike the previous ones discussed, favors pure strategists. The oak/maple game considered in the previous section is an N-player game played by members of a population of size N. The next case we shall consider is a game played as an encounter between two players. We will assume (as is common in discussions of this type) that each individual plays the game, without learning, against the other members of the population with sufficient frequency that the payoff to an individual is equal to the expectation of the payoff, given the population composition in that generation (Maynard Smith, 1988).

In a game of this type, each player faces not the mean population strategy, but the mean strategy of the *other* players in the population. In a finite population with the behaviors expressed in the equilibrium ratio, each pure strategist does not play against itself. Instead, it faces a subpopulation playing a strategy equal to the mean population strategy with its pure strategy subtracted. This subpopulation will naturally be impoverished with respect to that behavior, when compared to the original population.

This fact can, in certain circumstances, benefit the pure strategist over the mixed strategist. First, the game must be one in which a behavior is favored when the frequency of that behavior in the population is below equilibrium. This condition holds for the games in Sections 3–5 of this paper. Second, for the pure strategist to actually receive a higher payoff than the mixed strategist mixing behaviors according to the evolutionarily stable state, the population must express the equilibrium ratio of the two behaviors, or a ratio close enough that the removal of a single pure strategist places that behavior in the minority relative to equilibrium.[11] Under these conditions, a pure strategist will always be playing against a mixture of behaviors which is slightly impoverished with respect to its own behavior, compared to equilibrium. As it is encountering a mixture in which its own behavior is under-represented, it receives a payoff which is better than the equilibrium payoff. The mixed strategist playing the equilibrium mixture encounters the exact mixture of behaviors that characterizes the population at equilibrium, and consequently it receives the equilibrium payoff only.[12] It is important to note that this effect applies only to competition between pure strategists and individual behavior mixers. A developmental coin-flipping mixed strategist, by virtue of playing the same behavior for its entire life, also faces a population slightly impoverished with respect to its own behavior and consequently receives the same advantage enjoyed by a pure strategist. In the case of pure strategists/developmental coin-flipper competition, the only deterministic effect operating is the basic mixed strategy advantage.

We will call this the *don't play yourself effect* (abbreviated DPY). Perhaps the simplest model with illustrates this effect is a two-by-two game, the "anti-coordination team game."

4.1 The Model

Consider a population of asexual haploids playing the two-by-two game specified in Table 2. This game is an anti-coordination game because it is in the interest of both players not to coordinate (play the same strategy). We call it a team game because player 1 always receives the same payoff as player 2, regardless of the moves chosen by each, and thus the two players are acting as a team, splitting the total payoff equally. In the payoff matrix above, the lower case letters a and b represent particular behaviors. In a given population, consider three strategies: A strategists exhibit only behavior a, B strategists exhibit only behavior b, and mixed strategists I exhibit behavior a with frequency 1/2 and behavior b with frequency 1/2. Suppose first that the population is infinite so that there are no sampling effects. As in the oak/maple game, at equilibrium, each behavior will be expressed with frequency 1/2 in

Table 2. Payoff matrix for the team anti-coordination game.

	a	b
a	0	1
b	1	0

the population and each behavior is advantageous when rare. Once again there are various ways that this equilibrium can be reached at the level of strategies. There could be a polymorphism of A and B, each at a frequency of 0.5. Alternatively, the population could be monomorphic for I. Thirdly the population could contain some proportion of I strategists and the remainder be equally divided between A and B strategists. In an infinite population, selection does not distinguish among these alternatives. This is not the case in a finite population, however.

In order to examine the finite population case, we will write the dynamical system as we did earlier for the oak/maple game. Define x_1 as the fraction of A players, x_2 as the fraction of B players, and y as the fraction of I players in the population. Bear in mind the fact that x_1, x_2, and y are not continuous variables, because not all possible fractions can be expressed in a population with a finite number of individuals. In a population of size n, the non-normalized expected fitnesses of each type are given below.

$$w_A = x_2 + \frac{y}{2}$$
$$w_B = x_1 + \frac{y}{2} \tag{6}$$
$$w_I = \left(1 - \frac{1}{n}\right)\frac{1}{2}$$

The dynamic equations for this system can be written as follows.

$$\bar{w}x_1' = \left(x_2 + \frac{y}{2}\right)x_1$$
$$\bar{w}x_2' = \left(x_1 + \frac{y}{2}\right)x_2 \tag{7}$$
$$\bar{w}y' = \left(1 - \frac{1}{n}\right)\left(\frac{1}{2}\right)y$$

Here, x_1', x_2', and y' are the frequencies of the A, B, and I strategists after one generation, and $\bar{w}$ is the mean population fitness, equal to the sum of the

right hand sides of the above equations. Using the fact that $x_1 + x_2 + y = 1$ and defining d by $2d = x_2 - x_1$, this system can be written as follows.

$$
\begin{aligned}
x_1' &= \frac{(1/2 + d)(1/2 - d - y/2)}{1/2 - y/2n - 2d^2} \\
x_2' &= \frac{(1/2 - d)(1/2 + d - y/2)}{1/2 - y/2n - 2d^2} \\
y' &= \frac{(n - 1)y}{n - 4nd^2 - y}
\end{aligned}
\tag{8}
$$

Now, let μ_t be the ratio of pure strategists to mixed strategists in generation t, i.e., $\mu_t = (x_1 + x_2)/y = (1 - y)/y$. Applying the above equations for x_1', x_2', and y', algebra yields an equation for μ_{t+1} in terms of μ_t:

$$
\mu_{t+1} = \left(\frac{n}{n - 1} \right) \left(\mu_t - \frac{4d^2}{y} \right)
\tag{9}
$$

Notice that this equation is the same as the equivalent expression for the oak/maple game, except that in this case it is multiplied by $n/(n - 1)$; this extra coefficient represents the advantage had by pure strategists in not playing themselves. As d, the distance from equilibrium with respect to behaviors, approaches 0, μ_{t+1} approaches $n\mu_t/(n - 1)$, i.e., pure strategists have an advantage and their numbers increase. As $|d|$ increases, the value of μ_{t+1} will eventually fall below the value of μ_t, i.e., mixed strategists have the advantage and their numbers increase. This is because of the basic mixed strategy advantage.

This model, then, exhibits the interaction of two different deterministic effects. Pure strategists have an advantage near the equilibrium with respect to behaviors, because they do not play themselves, while mixed strategists have an advantage away from equilibrium because of the basic mixed strategy advantage.

The interaction of the two deterministic effects in this system is shown in Figure 2. The vectors describing the direction of selection favor mixed strategists away from the equilibrium, and favor pure strategists near the equilibrium.

5. The hawk/dove game

At last, we are ready to consider the hawk/dove game, used by previous authors as the primary vehicle for discussion of the issues considered in this
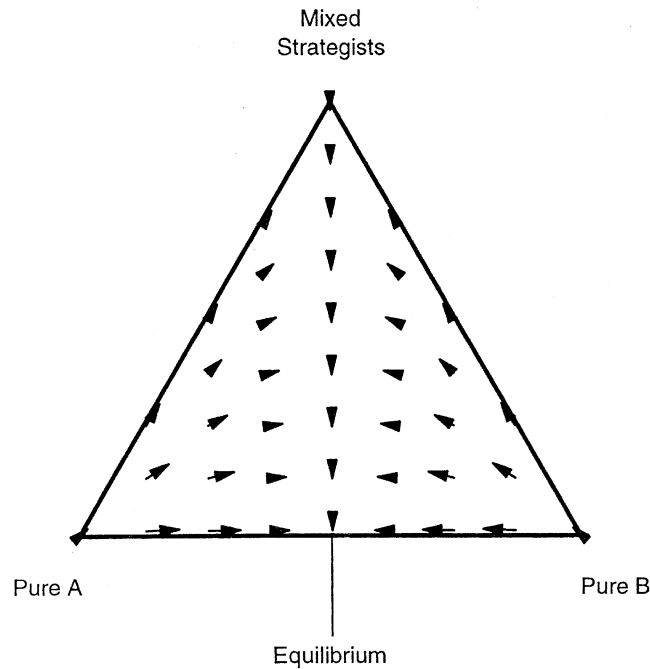
Figure 2. De Finetti diagram for the anti-coordination team game, $n = 20$.

paper. Again, we will suppose that there is a finite population of haploid individuals playing the game, in such a way that the payoff to an individual is equal to the expected payoff associated with that strategy, given the population composition in that generation. Like the anti-coordination team game, the hawk/dove game is a two-player game. It is not a team game, but instead has the following payoff matrix, where $a < c < d < b$:

Table 3. Payoff matrix for the hawk-dove game.

	Hawk	Dove
Hawk	a	b
Dove	c	d

In an infinite population, a lone hawk can always invade a population of doves, and similarly a lone dove can always invade a population of hawks. In fact, there is a single equilibrium ratio of behaviors, with the frequency of hawk behaviors equal to the following.

$$\hat{p} = \frac{(b - d)}{(b - d + c - a)} \tag{10}$$

Again, our discussion will compare two pure strategies with a single mixed strategy. The pure strategies are "always play hawk" and "always play dove." The mixed strategist plays hawk with a probability that corresponds to the equilibrium mixture of behaviors. The following system of equations specifies the dynamic for the infinite population hawk/dove game, where x_1 is the frequency of pure doves, x_2 is the frequency of pure hawks, y is the frequency of mixed strategists (playing the infinite population equilibrium mixture of behaviors), $\hat{p}$ is the fraction of hawk behaviors by mixed strategists playing the infinite population equilibrium, as given above, and the mean population fitness $\bar{w}$ is the sum of the right hand sides of the equations.

$$
\begin{aligned}
\bar{w}x'_1 &= x_1(dx_1 + cx_2 + (c\hat{p} + d(1-\hat{p}))y) \\
\bar{w}x'_2 &= x_2(bx_1 + ax_2 + (a\hat{p} + b(1-\hat{p}))y) \\
\bar{w}y' &= y((b\hat{p} + d(1-\hat{p}))x_1 + (a\hat{p} + c(1-\hat{p}))x_2 \\
&\quad + (a\hat{p}^2 + (b+c)\hat{p}(1-\hat{p}) + d(1-\hat{p})^2)y)
\end{aligned}
\tag{11}
$$

The dynamic equations for the *finite* hawk/dove game for a population of size n, with mixed strategists playing the finite population equilibrium $\hat{p}_f$ are given below.

$$
\begin{aligned}
\bar{w}x'_1 &= x_1\left(d\left(x_1 - \frac{1}{n}\right) + cx_2 + (c\hat{p}_f + d(1-\hat{p}_f))\,y\right) \\
\bar{w}x'_2 &= x_2\left(bx_1 + a\left(x_2 - \frac{1}{n}\right) + (a\hat{p}_f + b(1-\hat{p}_f))\,y\right) \\
\bar{w}y' &= y\left((b\hat{p}_f + d(1-\hat{p}_f))\,x_1 + (a\hat{p}_f + c(1-\hat{p}_f))\,x_2\right. \\
&\quad \left. + \left(a\hat{p}_f^2 + (b+c)\hat{p}_f(1-\hat{p}_f) + d(1-\hat{p}_f)^2\right)\left(y - \frac{1}{n}\right)\right)
\end{aligned}
\tag{12}
$$

Here the mixed strategists are playing the equilibrium mixture of behaviors for a finite population – this is not the same as the familiar infinite population equilibrium, as was pointed out by Schaffer (1988). In the finite case, the equilibrium mixture of behaviors is a function of population size and is equal to the following expression:

$$
\hat{p}_f = \frac{\frac{n-1}{n-2}b - d - \frac{1}{n-2}c}{b - d + c - a}
\tag{13}
$$

The dynamics of this system are quite interesting, despite the simplicity of the game itself. All four of the effects discussed so far in this paper have

an effect on the system, and their interaction is not straightforward. One reason for this is that, unlike the behaviors *oak* and *maple* or *a* and *b*, the two behaviors in the hawk/dove game, hawk and dove, are not symmetrical with respect to each other.

Firstly, this is a system in which both of the deterministic effects outlined earlier are found. When the population is some distance away from the equilibrium mixture of behaviors, the basic mixed strategy advantage applies.[13] Selection acts in favor of the mixed strategist. However, when the system is near equilibrium with respect to behaviors, the "don't play yourself" effect acts against mixed strategists. In the anti-coordination game discussed in Section 4, the DPY effect benefitted both pure strategies. In the hawk/dove game, however, all strategies do best when facing doves. Pure hawks do not have to play themselves, and instead face a population with more doves than that faced by mixed strategists or doves. For this reason, pure hawks receive a DPY advantage relative to mixed strategists and to doves. Mixed strategists likewise play a population with more doves than do doves, and receive a similar, though lesser, advantage relative to doves. Pure doves do not gain from the fact that they play more hawks, but they do better than other strategies in hawk-heavy populations.

The DPY effect not only aids hawks, but it also shifts the evolutionarily stable ratio of hawk to dove behaviors, as population size changes. This is why the finite population equilibrium behavior frequency is a function of population size, as noted above (Schaffer 1988). In a team game, $b = c$ and therefore the finite and infinite population equilibria are the same. In a game such as the hawk/dove game, a pure strategist playing the "selfish" strategy is able to invade the infinite population equilibrium, because it does not have to play itself. Though it does not increase its own payoff by playing the selfish strategy instead of the mixed strategy, it nonetheless decreases the payoff to the remaining individuals in the population by its choice of strategy, is more successful than the population average, and therefore successfully invades (Riley 1979).

The interaction of the two deterministic effects applicable to this system is illustrated in Figure 3. Mixed strategists are favored away from the equilibrium, while near equilibrium, the pure strategists are favored. This qualitative result holds regardless of whether the mixed strategists are playing the finite population equilibrium strategy or the infinite population equilibrium strategy.

In a finite population of this sort, the two stochastic effects we have discussed will also operate. Firstly, there is a co-dependence relation between the pure strategies. If either one of the pure strategies is lost, the other will probably be lost soon after, as it is then strongly selected against. Thus, this
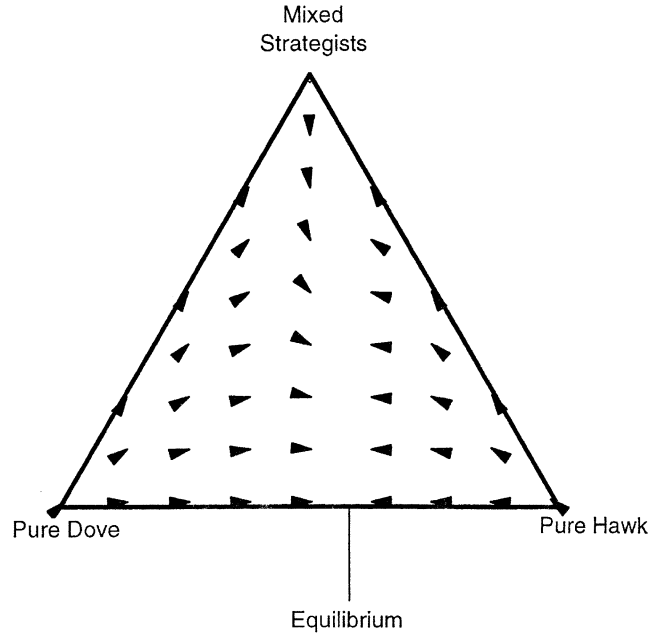
Figure 3. De Finetti diagram for the hawk/dove game, mixed strategists playing finite population equilibrium, $n = 20$, $a = 0$, $b = 3$, $c = 1$, $d = 2$.

effect favors the mixed strategists. Secondly, the geometric mean fitness effect will play a role. In the games discussed earlier, the strategy with the lowest fluctuations in fitness as frequencies change was the mixed strategy. In the hawk/dove game, however, it is the *pure dove* strategy that has the lowest level of fitness fluctuation and consequently receives the largest benefit from the geometric mean fitness effect. A pure hawk has the highest fluctuation – its payoff from an interaction is much more dependent on who it is paired with than is the payoff to a dove. Mixed strategists are between hawks and doves in this respect. The exact role of the two stochastic effects is difficult to discern and more work needs to be done here. Hawks, for example, are more severely affected when the population is unfavorable to them, but they will also bounce back very rapidly from a situation of low frequency.

To investigate the relationship between the four effects which should play a role in finite hawk/dove games, we made use of simulations. These simulations were modeled on work done for similar purposes by Maynard Smith (1988).

Maynard Smith's simulation makes use of a population which starts at a state in which there are 8 hawks, 7 doves, and 15 mixed strategists. The mixed strategists play the infinite population ESS mixture. The result is that there
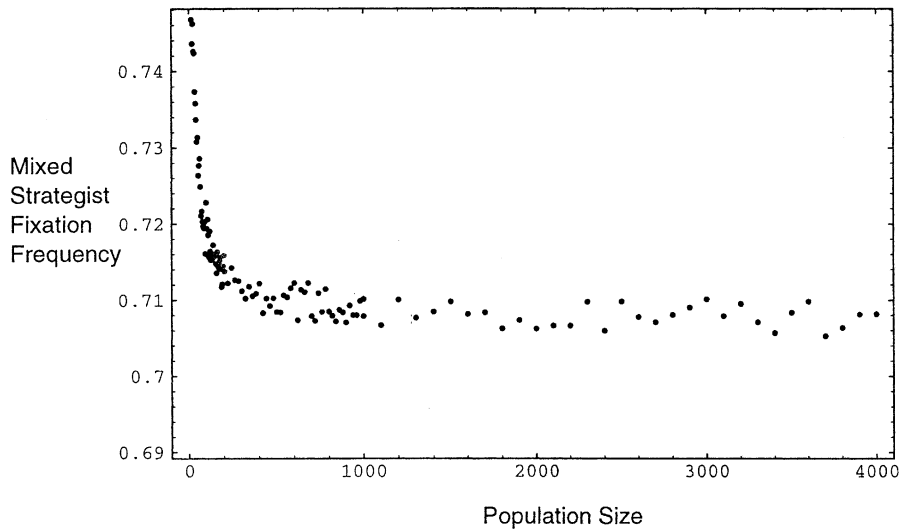
Figure 4. Fraction of mixed strategist fixations in the hawk/dove game, mixed strategists playing the finite population equilibrium, with 100,000 trials/point.

is a tendency for mixed strategists to win out over pure strategists. In 500 simulations, the pure strategists went extinct 380 times, or 76% of the time. We should note here that the starting point chosen by Maynard Smith may give an advantage to mixed strategists because of the codependence effect.[14]

We extended Maynard Smith's simulations to populations of size 12 through 4000, starting with 1/4 hawks, 1/4 doves, 1/2 mixed strategists, and conducting 100,000 trials for each population size. The fixation frequencies of mixed strategists for each population size are seen in Figure 4. In this figure, the mixed strategists are playing the finite population equilibrium for the appropriate size of population.

We found the same basic result as that reported by Maynard Smith: the mixed strategist is fixed more often. The results are qualitatively unaffected when the mixed strategists play the infinite population equilibrium instead of the appropriate finite population equilibrium. In both cases, the advantage associated with the mixed strategy is also relatively constant, decreasing only slightly as population size increases. It is interesting to notice that the fixation frequencies of mixed strategists in the finite population model do not appear to be converging to the fixation frequency in the infinite population model, even as population size goes to infinity.

An overall picture of the hawk/dove game in finite populations is gained by consideration of the two different methods we have used here. The deterministic analysis represented in Figure 3 gives part of the picture: there is an

interaction between the basic mixed strategy advantage and the DPY effect. The first of these effects is a general one, applying in all games featuring rare advantage. The second is more local in its application, applying to pure strategists competing against individual behavior mixers in games which can be modeled as a series of one-on-one interactions, but not necessarily in games which are modeled as a series of simultaneous interactions with the population at large, such as the oak/maple game in which one effectively "plays oneself." It is worth noticing that most "sex-ratio" games, in which an individual attempts to produce offspring in a fitness-maximizing sex ratio, are games in which one plays oneself and therefore such games will not feature this DPY effect.

A different perspective is gained by means of the simulations, which include stochastic factors as well as deterministic ones. As Vickery (1988)[15] and Hines and Anfossi (1990) demonstrated and we discussed in more detail, the purely deterministic dynamics, with no sampling-based fluctuations in strategy frequencies, strongly favor the pure strategists. In the stochastic simulations, however, we find that mixed strategists tend to have an overall advantage, one which is largely independent of population size, and also holds whether the finite population or the infinite population equilibrium mixture of behaviors is played by the mixed strategist. This leads to an important point: deterministic and stochastic methods can generate opposing predictions. The natural process of reproduction being an inherently stochastic process, this serves as a caution against over-generalizing from the results of purely deterministic models.

6. Conclusions

This study had several distinct aims. On the more scientific side, we sought a better understanding of the relationships between polymorphisms and individual mixed strategies, asking which we expect to see in a population, and why. On the more philosophical side, we sought to show that certain widely-used methods, which analyze only the distributions of behaviors and do not systematically treat the ways in which these distributions of behaviors are realized, leave some important questions unaddressed, questions about how properties like complexity and diversity are realized within and across individuals. We will say more about each of these topics in turn.

Mathematically, we have described four distinct effects which discriminate between individual-level and population-level realizations of behavioral heterogeneity; these effects are summarized in Table 4. Two of these effects are deterministic and two are stochastic. By this we mean that two of them concern simply the direction of selection, and two concern the consequences

Table 4. Selective effects influencing pure/mixed strategist competition.

Selective Effect	Type	Favors	First described by
Geometric mean fitness effect	stochastic	mixed/doves	Dempster (1955)
Basic mixed strategist advg.	deterministic	mixed	Hines (1980, 1987)
DPY effect	deterministic	pure/hawks	Riley (1979), Schaffer (1988)
Pure strategist codependence	stochastic	mixed	Vickery (1988)

of random fluctuation, as it interacts with selection. The deterministic effects are the *basic mixed strategy advantage* which favors mixed strategies, and the *don't play yourself (DPY)* effect, which favors pure strategies, or, in the case of the hawk/dove game, pure hawks. The anti-coordination team game and the finite hawk/dove game feature both of these effects. The oak/maple game features the basic mixed strategy advantage but not the DPY effect. The stochastic replicator dynamics model of Section 2 does not have either effect.

The two other effects described are stochastic: the *geometric mean fitness* effect and the *co-dependence* effect. Both of these effects favor the mixed strategy over pure strategies in the oak/maple and anti-coordination game; in the hawk/dove game, the geometric mean fitness effect favors pure doves. We have not analyzed these effects in as much detail as the others. The geometric mean fitness effect is easy to understand when it operates alone, as in the stochastic replicator dynamics model of Section 2. No other effect applies to that system. In the other games, however, it is more difficult to isolate the consequences of this effect from the consequences of the other effects discussed. This results from the fact that fitnesses are frequency dependent in the other games, and thus any fluctuation which places the system at some particular point in the space of frequencies will automatically have certain effects on fitness. Though we have not treated this effect in detail in the later models, we claim that it should play a role in all models discussed, as a consequence of the multiplicative nature of the relations between fitnesses which vary over time.

We also have not discussed the co-dependence effect in detail. This effect operates in all the models discussed except for the initial model, because in each of these models, a lone pure strategy is likely to be lost in the absence of its counterpart. One problem which must be addressed in a more detailed analysis of this effect is the fact that the pure strategists have an advantage when rare, so that they will "bounce back" from a low frequency. In contrast, the mixed strategist does not have any advantage from rarity per se; it only has an advantage if one or the other of the pure strategists is rare. Consequently, it does not bounce back with the same strength from a state of low frequency.

The four effects we have examined have all been discussed previously in some form. The geometric mean fitness effect dates from Dempster (1955)

and Verner (1965), the basic mixed strategy advantage has been discussed by Hines (1980), the DPY effect has been discussed by Riley (1979), Schaffer (1988), and Hines and Anfossi (1990), and the co-dependence effect was noted by Vickery (1988). Our aim here has been to explore a range of situations in which various combinations of these effects apply, to provide an explanation of *why* each occurs, and to put these diverse effects together, viewing them as components of a larger picture. An additional step, not yet taken, would be a detailed examination of the relative *magnitudes* of each selective effect; such an investigation would further aid in providing an explanation of the simulation results presented in Figure 4.

More philosophically, we have tried to press a certain set of questions into the foreground. These questions have the following form: *granted* that some particular model predicts variation or heterogeneity in behavior, *how* is this heterogeneity likely to be realized in the biological world? At what level – the individual, or the population – will the heterogeneity reside? These questions are neglected by some popular methods of analysis, including standard static ESS analysis. In a system as simple as the oak/maple game, for example, the machinery of standard ESS analysis is able to answer the question of what distribution of oak-behaviors and maple-behaviors is expected, but it is not able to tell us if there is any reason to expect a polymorphism of specialist behaviors or a monomorphic population of mixed strategists. A dynamic analysis is able to answer this question.

There is an important sense in which "evolutionarily stable strategy theory" is often a misnomer. In games of the type considered here, this theory describes evolutionarily stable distributions of *behaviors*, and does not address the realization of these distributions of behaviors. This class of games (called "degenerating" by Thomas (1984)) includes such paradigmatic cases as the ordinary hawk/dove game.

The DPY effect can be used to make this point vivid. In both the anti-coordination game and the hawk/dove game, in a finite population, the system can be at or very close to equilibrium with respect to the distribution of behaviors and yet *still be undergoing evolutionary change*. While the system sits at equilibrium with respect to behaviors, the mixed strategist is steadily being selected against (see Figure 2). The mixed strategist can be lost – a particular realization of biological complexity can be eliminated from the population – while the population remains "at or near equilibrium" with respect to the distribution of behaviors.

This is not an *inconsistency* in the basic ESS theory; the framework selects one type of question, and makes strong idealizations in addressing it. Further, the DPY effect, which we use to make this point, only applies in a finite population, while ESS theory is usually intended to describe infinite populations.

As this case shows, however, the predicted evolutionary outcome in a large finite population can differ in biologically important ways from the predicted outcome in an infinite population.

When particular methods become popular, some questions are pushed into positions of prominence and others are relegated to minor roles. ESS methods study the distributions of behaviors, and push the issue of the realization of these distributions back into the wings. Our aim has been to bring the issue of realization into center stage.

Acknowledgements

Notes

[1] The consequences of this feature of Levins' model are discussed in Seger and Brockmann (1987) and Godfrey-Smith (1996).

[2] Non-degenerating models may predict variety which cannot be realized by population level expression of the mixed strategy, i.e., by a polymorphism of pure strategists. For example, a mixed strategy may be maintained by the trade-off between individual benefits and group costs of a particular action. In local resource competition models (Clark 1978), producing the non-dispersive sex provides an individual benefit, for this is the rarer sex, and a group cost, in that all individuals in the group must later compete with this individual (Orzack 1993, personal communication). Similarly, begging nestlings may experience an individual benefit in terms of an increased probability of being fed, and a group cost in terms of increased predation risk for the nest (Godfray and Parker 1992). Under these circumstances, individuals playing the pure strategy with no individual benefit and no group cost will be out-competed by individuals playing the pure strategy with individual benefit and group cost. Thus the mixed equilibrium is unstable when it occurs at the population level; instead we expect to find each individual expressing the equilibrium mixed strategy.

[3] Here, we modify the terminology of Cooper and Kaplan (1982), who termed this *adaptive coin flipping*.

[4] For a discussion of the formal definition of evolutionarily stable strategies, see Hines (1987).

[5] Gillespie (1991) summarizes and extends the previous work on this problem.

[6] For any actual sequence of years, the relative rate of increase of a genotype in a haploid model is given by its geometric mean fitness where the weighting is done by the frequencies of the different types of years in the sequence. It is also possible to construct a model in which the underlying probabilities of different types of years are used, rather than their actual frequencies. In that case it is necessary to take into account all of the possible sequences of years when computing expected fitness. In this section, however, we will restrict our discussion

to the simpler type of model, using the actual frequencies of different events in a sequence of years or trials. This simpler type of model is sufficient to illustrate the key phenomenon.

[7] It is important to distinguish the mixed strategists in this model, which always forage from each source half the time, from generalists which can choose to forage in the less depleted area. Wilson and Yoshimura (1994) present a model of the latter type.

[8] When the population under consideration is finite, not all points on the simplex are actually attainable. This is not a problem, in that the diagram describes the direction of selection at *all* points, a subset of which are the ones possible in a finite population of a given size.

[9] To see this, start with a population with three neutral types: O, M, and I, in fractions 1/4, 1/4, and 1/2 respectively. Break the I players into two groups, I_1 and I_2. If either the O group or the M group goes extinct before both I groups are lost, the pure strategists are doomed. Since the types are neutral with respect to one another when all are present, the probability of losing O or M first is 1/2; conditional that this has not occurred, the probability of losing O or M second is 2/3. Therefore, the probability of losing neither O nor M first or second is 5/6; this is the probability of the pure strategists outlasting the mixed strategists composing the two I groups. Computer simulations of the neutral case, for finite population sizes with O, M, and I populations chosen from a trinomial distribution, confirm this result.

[10] This effect complicates the process of defining exactly when mixed strategists are "outperforming" pure strategists. Often, "outperforming" is based on fixation probabilities for non-frequency dependent selection; type A outperforms the other types when, starting with frequency x in the population, it is fixed with probability $y > x$. While this definition can be applied to pure/mixed competition, it does not seem entirely adequate, because of the pure strategist codependence effect. By this definition, in a model which is selectively neutral when all types are present, mixed strategists still drastically "outperform" pure strategists. One way around this problem is to consider populations which feature mutation. In a neutral model with mutation, the expected proportion of a given strategy is equal to the proportion of mutations to that strategy. A strategy could be said to outperform the other strategies whenever the mean frequency of that strategy exceeds the proportion of mutations to the strategy. This approach has not yet been used in treating pure/mixed strategist competition.

[11] Even when this second condition does not hold, the pure strategists are aided by this effect. However, if this second condition is not met, this advantage is not great enough to give *both* pure strategist types a higher payoff than that of the mixed strategist.

[12] Schaffer (1988) describes a consequence of this effect for the hawk/dove game (to be discussed in the next section). He notes that in a finite population of individuals playing the repeated hawk/dove game, any mixed strategy equilibrium can be invaded by a pair of other strategies that "frame" the equilibrium, one playing hawk more frequently and the other playing hawk less frequently.

[13] Hines (1987, 1980) notes the application of the basic mixed strategy advantage to hawk/dove games. His discussion shows that the effect always applies when the system is away from equilibrium, if the population is *infinite*. Sober (1993) and Orzack and Sober (1994) appear to apply this result, or one like it, to finite populations. In a finite population, however, this effect can be outweighed by the DPY effect discussed in this paper. This can be seen by counter-example. Consider a population playing the hawk/dove game with payoff parameters $a = 0, b = 3, c = 1$, and $d = 2$. The evolutionary stable strategy (in an infinite population) for this population is one half hawk, one half dove. Consider a population with three hawks, two doves, and one mixed strategist playing (1/2, 1/2). The average population fitness exceeds the fitness of the mixed strategist playing the ESS. Even when the mixed strategist is playing the finite-population ESS, 3/4 hawk in this case, it has a lower fitness than the population average.

[14] Maynard Smith also offers a heuristic argument for the success of the mixed strategists, based on a measure of geometric mean fitness which, in our view, is not correct. He compares a polymorphism to a mixed strategy in the following way: the geometric mean fitness of the hawk and dove strategies, *within* a year, is compared to the geometric mean fitness of the mixed strategy within a year. However, the appropriate way to make use of geometric mean fitnesses in this situation is to compare the geometric mean fitnesses of each of the various

strategies *across* years, as we did in Section 2. This is the style of analysis used in the models of Dempster (1955), Haldane and Jayakar (1963), Gillespie (1973), and the other authors mentioned earlier. Our criticism of Maynard Smith on this point is necessarily qualified by the fact that he introduces his geometric mean argument very tentatively.

[15] Vickery (1988) reports the results of simulations which resemble those of Maynard Smith (1988), but which remove the stochastic factors associated with reproduction. The representation of a strategy in the next generation is exactly proportional to its fitness in the present generation. Under these conditions, mixed strategists always went to extinction. This is predicted by our analysis; if there are no stochastic fluctuations associated with reproduction, then the system will move to the equilibrium ratio of behaviors and stay there, and as it does so the DPY effect will lead to the extinction of the mixed strategists.

References

Clark, A.B.: 1978, 'Sex Ratio and Local Resource Competition in a Prosimian Primate', *Science* **201**, 163–165.

Cooper, W.S. and Kaplan, R.H.: 1982, 'Adaptive "Coin-Flipping"; a Decision-theoretic Examination of Natural Selection for Random Individual Variation', *Journal of Theoretical Biology* **94**, 135–151.

Dempster, E.R.: 1955, 'Maintenance of genetic hetergeneity', *Cold Spring Harbor Symposium on Quantitative Biology* **20**, 25–32.

Gillespie, J.: 1973, 'Polymorphism in random environments', *Theoretical Population Biology* **4**, 193–195.

Gillespie, J.H.: 1991, *The Causes of Molecular Evolution*, Oxford Series in Ecology and Evolution. Oxford University Press, New York.

Godfray, H.C.J. and Parker, G.A.: 1992, 'Sibling competition, parent-offspring conflict, and clutch size', *Animal Behaviour* **43**, 473–490.

Godfrey-Smith, P.: 1996, *Complexity and the Function of Mind in Nature*, Cambridge University Press, Cambridge.

Haldane, J.B.S. and Jayakar, S.D.: 1963, 'Polymorphism due to selection of varying direction', *Journal of Genetics* **58**, 237–242.

Hartl, D.L. and Cook, R.D.: 1973, 'Balanced polymorphisms of quasineutral alleles', *Theoretical Population Biology* **4**, 163–172.

Hines, W.G.S.: 1980, 'Strategy stability in complex populations', *Journal of Applied Probability* **17**, 600–610.

Hines, W.G.S.: 1987, 'Evolutionary Stable Strategies: A Review of Basic Theory', *Theoretical Population Biology* **31**, 195–272.

Hines, W.G.S. and Anfossi, D.: 1990, 'A discussion of evolutionarily stable strategies', in S. Lessard (ed.), *Mathematical and Statistical Developments of Evolutionary Theory*, Kluwer Academic Publishers, Dordrecht, pp. 229–267.

Karlin, S. and Lieberman, U.: 1974, 'Random temporal variation in selection intensities: case of large population size', *Theoretical Population Biology* **6**, 355–382.

Levins, R.: 1968, *Evolution in Changing Environments*, Princeton University Press, Princeton.

Maynard Smith, J.: 1982, *Evolution and the Theory of Games*, Cambridge University Press, Cambridge.

Maynard Smith, J.: 1988, 'Can a mixed strategy be stable in a finite population?', *Journal of Theoretical Biology* **130**, 247–251.

Maynard Smith, J. and Price, G.R.: 1973, 'The logic of animal conflict', *Nature* **246**, 15–18.

Orzack, S.H. and Sober, E.: 1994, 'Optimality models and the test of adaptationism', *American Naturalist* **143**(3), 361–380.

Riley, J.G.: 1979, 'Evolutionary equilibrium strategies', *Journal of Theoretical Biology* **76**, 109–123.

Schaffer, M.E.: 1988, 'Evolutionarily Stable Strategies for a Finite Population and a Variable Contest Size', *Journal of Theoretical Biology* **132**, 469–478.

Seger J. and Brockmann, J.: 1987, 'What is bet-hedging?', *Oxford Surveys in Evolutionary Biology* **4**, 182–211.

Sober, E.: 1993, *Philosophy of Biology*, Dimensions of Philosophy Series. Westview Press, Boulder.

Thomas, B.: 1984, 'Evolutionary Stability: States and Strategies', *Theoretical Population Biology* **26**, 49–67.

Verner, J.: 1965, 'Selection for sex ratio', *American Naturalist* **94**, 419.

Vickery, W.L.: 1988, 'Reply to Maynard Smith', *Journal of Theoretical Biology* **132**, 375–378.

Wilson, D.S. and Yoshimura, J.: 1994, 'On the coexistence of specialists and generalists', *American Naturalist* **144**(4), 692–707.