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THE EVOLUTION OF STRATEGY VARIATION: WILL AN ESS EVOLVE?

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Abstract.—Evolutionarily stable strategy (ESS) models are widely viewed as predicting the strategy of an individual that when monomorphic or nearly so prevents a mutant with any other strategy from entering the population. In fact, the prediction of some of these models is ambiguous when the predicted strategy is ''mixed'', as in the case of a sex ratio, which may be regarded as a mixture of the subtraits ''produce a daughter'' and ''produce a son.'' Some models predict only that such a mixture be manifested by the population as a whole, that is, as an ''evolutionarily stable state''; consequently, strategy monomorphism or polymorphism is consistent with the prediction. The hawk-dove game and the sex-ratio game in a panmictic population are models that make such a ''degenerate'' prediction. We show here that the incorporation of population finiteness into degenerate models has effects for and against the evolution of a monomorphism (an ESS) that are of equal order in the population size, so that no one effect can be said to predominate. Therefore, we used Monte Carlo simulations to determine the probability that a finite population evolves to an ESS as opposed to a polymorphism. We show that the probability that an ESS will evolve is generally much less than has been reported and that this probability depends on the population size, the type of competition among individuals, and the number of and distribution of strategies in the initial population. We also demonstrate how the strength of natural selection on strategies can increase as population size decreases. This inverse dependency underscores the incorrectness of Fisher's and Wright's assumption that there is just one qualitative relationship between population size and the intensity of natural selection.

Key words.—Evolutionarily stable state, evolutionarily stable strategy, game theory, genetic drift, natural selection, population size.

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Traits for which the fitness of an individual is usually frequency dependent, such as sex ratio, have received substantial theoretical and empirical study in recent decades, with much of the theoretical study involving game-theoretic models. The most famous example of such an approach is the evolutionarily stable strategy (ESS) analysis developed by Maynard Smith and Price (1973). Such a strategy is evolutionarily stable in the sense that when almost all individuals in a population possess it, a rare mutant individual possessing another strategy cannot possess a selective advantage. This concept has been extensively developed (for theoretical elaboration, see Maynard Smith 1982; Hines 1987, 1990; Hofbauer and Sigmund 1998; and for applications to natural populations, see Dugatkin and Reeve 2000.) In what follows, the term ''ESS strategy'' will refer to the strategy of an individual predicted by an ESS model and the term ''ESS'' will refer to a population in which all individuals possess an ESS strategy.

Although the definition of an ESS involves uniformity (save for rare mutants) there are different ways in which an ESS can be reconciled with within-population variation. Consider an ESS strategy that is a mixture of subtraits. A sex ratio, for example, may be viewed as such a mixed strategy, with a mother sometimes expressing one subtrait (produce a daughter) and sometimes the other (produce a son). To this extent, a snapshot of a population could record variation since one mother might be seen producing a daughter while another might be seen producing a son, even though both mothers produce the same sex ratio over their reproductive lifetimes.

The second way in which an ESS can be reconciled with variation relates to the fact that some ESS models that predict a mixture of subtraits do not uniquely predict an ESS. Instead, they predict only the equilibrium mixture expressed by the population and do not predict the mixture produced by any given individual. To this extent, the equilibrium mixture of subtraits could be manifested as an ESS or as a mixture of individuals that differ from one another in the subtrait mixtures they express during their lifetimes. At the extreme, this mixture of individuals would be a mixture of pure strategists, that is, individuals that never change the subtrait they express. For example, in the case of a sex ratio, this configuration would be an equal mixture of two types of mothers, one type producing only daughters and the other only sons (for related discussions, see Patterson 1928; Metz 1938; West et al. 1999).

The set of models that have ambiguous predictions about the manifestation of individual strategies includes the sex-ratio model for a panmictic population (Kolman 1960; Poethke 1988; see also Verner 1965), the hawk-dove model (Maynard Smith 1976), and the digging-entering model of nesting behavior (Brockmann et al. 1979). Thomas (1984) defined such models as being ''degenerate'' and called their ambiguous prediction an ''evolutionarily stable state''; in contrast, those models predicting an ESS are defined as ''nondegenerate.'' Well-known examples of the latter kind of model concern the sex ratio expressed in a population with local mate competition (e.g., Hamilton 1967; Frank 1985; Herre 1985). These models predict that the optimal sex ratio be expressed by each individual; illustrations of the selective disadvantage of non-ESS sex ratios are shown below and in Orzack et al. (1991) and West and Herre (1998).

It is a truism that the classification of any given model as degenerate or nondegenerate reflects its mathematical formulation. Thomas's (1984) classification of the hawk-dove model as degenerate rests upon Maynard Smith's model formulation, which omits some features whose presence is often thought of as essential for the sake of biological reality. For example, this formulation ignores the fact that populations are finite in size. In this paper, we investigate whether incorporation of population finiteness into a degenerate strategic model changes its equilibrium from an evolutionarily stable state to an ESS (or to another configuration).

This question has been addressed by Vickery (1987, 1988), Maynard Smith (1988), and Bergstrom and Godfrey-Smith (1998). Their conclusion is that an ESS is likely to evolve in a finite population. This conclusion is based on Monte Carlo simulations in which the ESS strategy was fixed in approximately 70% or more of populations studied (see Maynard Smith 1988, p. 250; Bergstrom and Godfrey Smith 1998, p. 224).

We first describe our population model, then we outline analytical results relating to the evolutionary consequences of finite populations, and finally we describe our simulation results.

THE POPULATION MODEL

We define a ''dynamical'' model as one that includes an explicit mechanism by which traits are transmitted from one generation or time unit to the next. A dynamical game-theoretic model of the evolution of strategies differs from a standard model of frequency-dependent trait evolution as formulated by population geneticists only in that the former has explicit elaboration of the process by which individuals express their interactive traits. Analysis of either kind of model requires an assumption as whether the population is finite or infinite in size. We assume here that there are N haploid individuals in a panmictic population with nonoverlapping generations. An individual with genotype i always manifests strategy i; hereafter, we use the latter term only. Within a given generation, there is first a competitive period during which individuals engage in pairwise contests where they express their strategies and then a reproductive period during which the strategy configuration for the next generation is formed. We further assume that the costs and benefits of expressing any strategy are temporally invariant. This formulation is standard (e.g., Hines 1987, pp. 197–198).

To fully determine the nature of the competitive period, one must decide how many contests each individual engages in. We consider two extreme cases. In the infinite contest (IC) case, each individual has an infinite number of pairwise contests with each other member of the population; in the single contest (SC) case, each individual has a single pairwise contest. We assume that the payoffs stemming from a given contest are constant. The IC case is the usual choice in the analysis of ESS strategy dynamics; it means that identical individuals have identical competitive experiences (since there is no random sampling to assemble the set of opponents faced by any individual.)

In the reproductive period, the production of offspring to form the next generation occurs via the replicator dynamic described by Taylor and Jonker (1978). The expected contribution of offspring to the next generation by any given individual is strictly proportional to the winnings accrued during the competitive period, although the random choice of individuals to form the next generation (genetic drift, as described by the Wright-Fisher model of reproduction) almost certainly causes the expected and realized contributions of offspring to differ.

ANALYTICAL RESULTS CONCERNING THE EFFECTS OF POPULATION FINITENESS ON STRATEGY EVOLUTION

A Deterministic Consequence of Population Finiteness

Riley (1979) noted that in a finite population the frequency of any individual's competitors identical to it is decreased (by $1/N$, where N is population size) as compared to the relative frequency in an infinite population, and the frequency of opponents that are different is correspondingly enriched (see also Vickery 1987). For a model predicting a mixed ESS strategy, when the population mixture is at or near the evolutionarily stable state it is straightforward to show that the evolutionary consequence of this ''don't play yourself'' (DPY) effect (Bergstrom and Godfrey-Smith 1998) can be to favor extreme strategies (e.g., pure hawk or dove as opposed to a mixed hawk-dove strategy, one-sex broods as opposed to two-sex broods, etc.), thereby discouraging evolution toward the ESS. For example, in a hawk-dove game in a finite population, a hawk benefits in such a circumstance from having fewer contests with hawks than non-hawk strategists do and thereby has a higher fitness than it would have in an identical infinite population. Figure 1 shows the differences in absolute fitness caused by the DPY effect for the hawk-dove game. It is well known that the magnitude of this effect is dependent in a simple way on the size of the population (e.g., Hines 1987, p. 217), and is $O(1/N)$. By its nature, the DPY effect concerns a comparison of fitnesses within a discrete generation and does not address the additional consequences of population finiteness on the transmission of strategies from generation to generation. To this extent, this effect alone is not definitive with respect to answering the question as to whether the ESS tends to evolve in a finite population.

The Stochastic Consequences of Population Finiteness

We consider two types of stochastic effects—those that occur during competition and those that occur during reproduction. The two cases of competition described above, IC and SC, differ in their degree of stochasticity as measured by among-individual differences in competitive experiences. In the IC case, since each individual has an infinite number of contests with each other individual, competitive stochasticity due to finiteness is absent and one can determine the exact payoff for any individual. In contrast, in the SC case competitive stochasticity is maximal, since each individual has a single contest with only one individual. The payoff for each individual will depend strongly on the random choice of opponent and on the random choices of action by each individual in the single contest. Because an individual always has only one opponent, variability at the level of the contest (payoff per individual against a given opponent) is unaffected by changes in population size. However, the variance of the

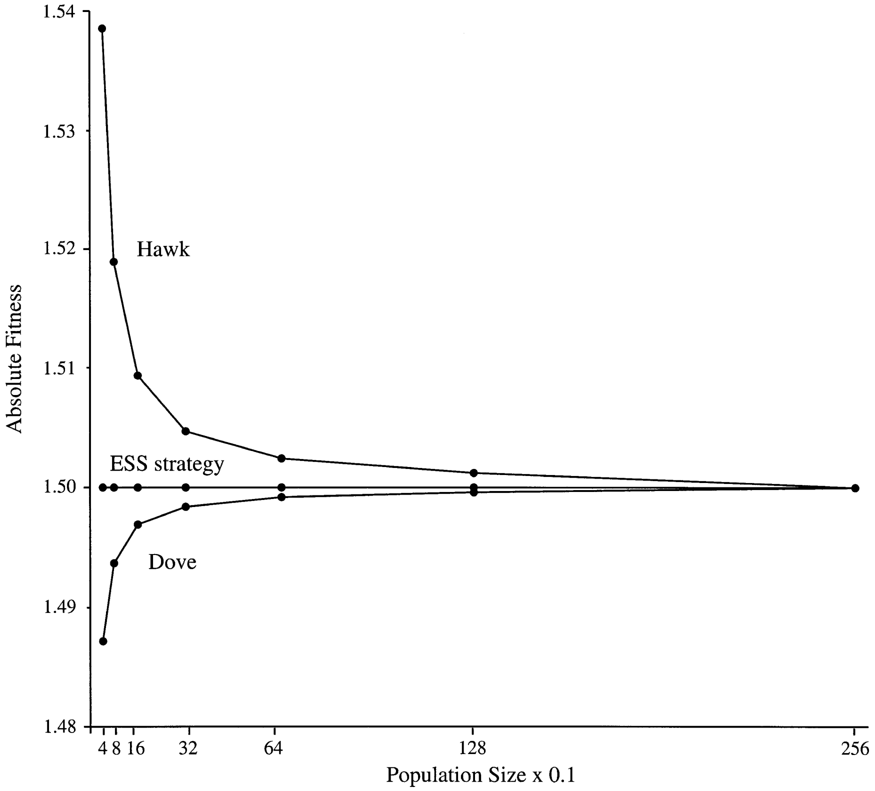

FIG. 1. Absolute fitnesses of the pure hawk, the pure dove, and the evolutionarily stable strategies as a function of population size. Fitness differences are the result of the ''don't play yourself'' effect, which stems from the absence for any given individual of its own strategy from the pool of contest opponents. The payoffs used are 0 and 3 for hawk played against hawk and dove and 1 and 2 for dove played against hawk and dove. For any given population size, we assume that there are 25% hawks, 25% doves, and 50% ESS strategists.

mean of such winnings is dependent on population size; it is straightforward to show that this variance is $O(1/N)$.

The effects of reproductive stochasticity can be substantial. When individuals differ little (or not at all) in the selective consequences of their strategies, the average within-population variance of strategies is expected to decline every generation simply due to genetic drift. The change is of order $O(1/N)$ (e.g., Ewens 2004, pp. 92–99). It is straightforward to show that this dynamic can result in extreme strategies attaining transient frequencies that cause the ESS strategy to have a selective advantage during competition.

When individuals differ more substantially in the selective consequences of their strategies (although not markedly so), the combined effect of stochasticity on competitive interactions and on reproduction can be approximately analyzed as follows.

Let strategy i be represented by u_i, a vector of the probabilities of playing each of the possible subtraits (such as hawk and dove). Define $p_t(u_i)$ as the frequency of strategy u_i at the beginning of generation t, $\phi_t(u_i)$ as the expected growth rate of u_i at generation t (= $\mathrm{E}[p_{t+1}(u_i)]/p_t(u_i)$, where E[] denotes expectation), and $\hat{\phi}_t(u_i) = p_{t+1}(u_i)/p_t(u_i)$ as the realized growth rate of u_i at generation t. Any discrepancy between $\phi_t(u_i)$ and $\hat{\phi}_t(u_i)$ reflects random sampling of offspring at the end of the reproductive period during the formation of the next generation. Following Taylor and Jonker (1978), one has

$$p_{t+1}(u_i) = \hat{\phi}_t(u_i)\hat{\phi}_{t-1}(u_i)\hat{\phi}_{t-2}(u_i) \cdots \hat{\phi}_2(u_i)\hat{\phi}_1(u_i)p_1(u_i), \quad (1)$$

so that

$$\log[p_{t+1}(u_i)] = \sum_{r=1}^{t} \log[\hat{\phi}_r(u_i)] + \log[p_1(u_i)], \quad (2)$$

which depends increasingly on the first term as time passes (assuming that $p_1[u_i]$ is positive). If $\hat{\phi}_t(u_i)$ is a continuous, differentiable, function in u_i and if selection favors individuals with a specific strategy, say u^*, then Taylor's theorem indicates that

$$\log[p_{t+1}(u_i)] \approx \sum_{r=1}^{t} a_r + (u_i - u^*) \sum_{r=1}^{t} b_r + (u_i - u^*)^2 \sum_{r=1}^{t} c_r + \log[p_1(u_i)], \quad (3)$$

where a_r, b_r, and c_r are constants. If t is large enough that $\log[p_1(u_t)]$ is small as compared to the latter two sums, then the density function of $p_{t+1}(u_t)$ is proportional to

$$D_{t+1}\exp\left[(u_i - u^*) \sum_{r=1}^{t} b_r + (u_i - u^*)^2 \sum_{r=1}^{t} c_r\right], \quad (4)$$

where D_{t+1} is a normalizing constant. This is the density function of a normal distribution with mean

$$-\frac{\sum_{r=1}^{t} b_r}{2\sum_{r=1}^{t} c_r} \tag{5}$$

and variance

$$-\frac{1}{2\sum_{r=1}^{t} c_r}. \tag{6}$$

We note that $\Sigma\ c_r$ is negative when selection acts against extreme strategies, thereby ensuring that the variance is positive. Accordingly, the frequency distribution of strategies tends to look like a normal distribution as the population evolves; this is a mock central-limit theorem. The favored strategy, u^*, may be the ESS strategy (or a strategy close to it) since one can show that individuals possessing it in infinite populations that are not at equilibrium have higher than average fitness (Hines 1980, pp. 607–608; Hines 1987, p. 205); this advantage decreases as the population gets closer to equilibrium. What this convergence to a normal-like distribution of strategy frequencies means is that a population starting with, for instance, a uniform strategy distribution that includes all possible strategies (pure and mixed) is expected to transiently develop a bell-shaped strategy distribution that is centered roughly around the ESS strategy. (Of course, the distribution differs from a normal distribution because it is discrete and has persistent gaps for strategies that are lost.) This distribution eventually decays to a monomorphism and the ESS strategy (or a similar strategy) is fixed with high probability unless it is lost as a result of random sampling during the reproductive period. If it is lost (or was not initially present), the population can evolve to a polymorphism of strategies (e.g., a pair of strategies) whose combined expression approximates the evolutionarily stable state. None of the constituent strategies need be close to the ESS strategy.

As in the case of the DPY effect, this heuristic argument is not definitive with respect to whether an ESS will evolve, as it is consistent with the possibility that some other strategies have higher fitnesses than the ESS strategy and accordingly, that they could be fixed in the population. We note that the inclusion of temporal variability in the payoffs is expected to increase a tendency for the ESS to evolve (Hines 1982).

Overview

We have shown that each of a number of important consequences of population finiteness has effects of order $O(1/N)$, so that it is impossible to resolve which is more important in a finite population by the device of comparing the orders of their effects. In addition, our analysis of the effects of natural selection and genetic drift suggest that finite populations will tend to evolve to the ESS, but this analysis is not compelling enough to be conclusive. Therefore, we used Monte Carlo simulations to assess the probability that a finite population becomes fixed for a single strategy and to determine whether this strategy is the ESS strategy.

MONTE CARLO SIMULATIONS

We simulated the hawk-dove game, with payoffs of 0 and 3 for hawk played against hawk and dove and 1 and 2 for dove played against hawk and dove, respectively. For both the IC case and the SC case, if one assumes that the population size is infinite, one can show that the ESS strategy is 0.5, that is, it consists of 50% of the hawk subtrait and 50% of the dove subtrait. We assumed that this prediction would apply to the finite dynamical system we simulated (see below for further discussion). The simulations were designed to assess how the probability that an ESS will evolve is affected by the population size, the initial numbers and frequencies of possible strategies, and the type of competition. Strategies were defined in terms of the probability of playing the hawk subtrait of

$$\frac{0}{m-1},\ \frac{1}{m-1},\ \frac{2}{m-1},\ \ldots,\ \frac{m-1}{m-1},$$

where $m = 5$, 9, 17, and 33 is the number of possible strategies in the initial population. Since m was always odd, a population could contain individuals with the ESS strategy (0.5). All possible initial frequencies of the m strategies were sampled from a uniform Dirichlet distribution by generating $m - 1$ uniform random variates to create random locations on the interval [0, 1]. These locations formed the endpoints of the intervals whose lengths matched the m probabilities with which each of the N individuals was assigned independently to strategy 1, 2, . . . , m. This way of creating initial strategy distributions meant that they were sampled from all possible initial distributions, including those far from the evolutionarily stable state.

Each simulated population underwent a competitive period followed by a reproductive period in each generation (see above for details). The composition of each population was assessed every 1000 generations. At such a time, the population was continued if more than two strategies were present, or if it was the first time only two strategies were present. A population was stopped if it was monomorphic or if it was the second time at which only two strategies were present (the assumption being that natural selection had ceased).

Our simulations were broader in scope than the simulations of Maynard Smith (1988) and Bergstrom and Godfrey Smith (1998). Their simulations involved only what we call the IC case and always started with the same fixed proportions of three strategies whose combined strategy expression was close to or coincident with the evolutionarily stable state for the given payoffs (= 0.5). (Maynard Smith used populations of size 30 having 8 hawks, 7 doves, and 15 ESS strategists. Bergstrom and Godfrey Smith used populations with sizes ranging from 12 to 4000, but always with 25% hawks, 25% doves, and 50% ESS strategists.)

There is some subtlety associated with the measurement of the probability that a population evolves to an ESS. It stems from the fact that the predicted ESS strategy (0.5) was derived from models (IC and SC) in which the population size was infinite, meaning that there were no effects of finiteness on reproduction in these models. Nonetheless, we applied their predictions to a dynamical system in which finiteness affected reproduction (via genetic drift).

There is an analysis of the hawk-dove game (Schaffer 1988) in which the number of individuals is finite; each has an infinite number of contests with each of the other individuals (as in the IC model). His analysis omitted consideration of the effects of finiteness on reproduction. For a given payoff matrix, Schaffer showed that the ESS mixed strategy is more hawklike than the ESS mixed strategy derived from the infinite population model. The difference between the two declines as population size increases. Following Maynard Smith (1998) and Bergstrom and Godfrey Smith, (1998) we chose not to use Schaffer's finite prediction; it differs little from the infinite prediction (= 0.5). For the smallest population size we used $N = 30$, the difference between the finite prediction and the infinite prediction is approximately 0.036. If Schaffer's ESS strategy is the ESS strategy for the IC or the SC dynamical system (with reproductive dynamics that include genetic drift), our choice means that the exact ESS strategy was not present in our simulations. Circumstantial evidence suggests that Schaffer's prediction is the exact strategy in our IC simulations. S. Lessard (pers. comm.) showed that this prediction is the ESS strategy when there is weak selection, and Wild and Taylor (2004) showed that it is the ESS strategy when reproductive dynamics are described by the Moran model (for a description of this model see Ewens 2004). Hence, we believe that the exact ESS strategy is very close to or identical to Schaffer's prediction, which in turn is very close to the value we used, 0.5. In addition, our simulation results for the SC dynamical system are also consistent with the belief that Schaffer's prediction is very close to the exact ESS strategy (see below.)

The preceding considerations concerning the ambiguity as to the exact ESS strategy for the dynamical systems we studied led us to use four different ways to assess the probability that a population evolves to a monomorphism such as an ESS.

The first way was to count the times that a population became monomorphic for any strategy. As a result, monomorphisms for pure strategies are included, although they are rare (even for small population sizes). This resulting probability was called the least strict (LS). The second way was to count the times that a population became monomorphic for any mixed strategy; the resulting probability was called strict (S). The third way was to count the times that a population became monomorphic for the infinite-population ESS strategy, the strategy ''to its left,'' and the strategy ''to its right''; the motivation being the presumption that this set brackets the true ESS strategy for the dynamical system. For example, if there are nine strategies, these central strategies are 0.375, 0.5, and 0.625. This way of assessing the probability was called more strict (MS). The fourth way was to count the times that the population became monomorphic for the infinite-population ESS strategy (0.5); this way was called completely strict (CS).

We carried out two simulations for both the IC and SC cases. The first contained a broad range of strategy numbers and of population sizes to get an overview of evolutionary dynamics. For each combination of strategy number and population size we used the LS way of measuring the probability that an ESS evolves. A statistical contrast measuring quadratic curvature was calculated for each initial distribution (ignoring missing values), so that we could assess the effect of the shape of the initial distribution on the evolutionary outcome by comparing the average contrast value of initial distributions leading to monomorphism and those leading to polymorphism.

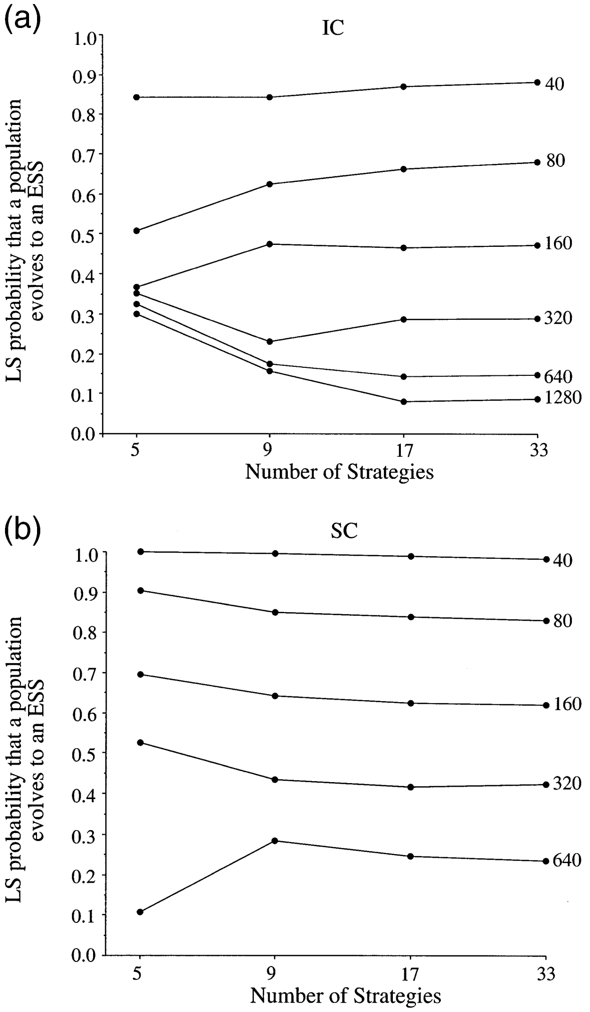

FIG. 2. The least strict (LS) probability that the population evolves to an ESS as measured in the first simulation. The probability is shown as a function of initial population size (40, 80, 160, 320, 640, and 1280) and number of possible strategies (5, 9, 17, and 33). (a) The infinite contest case, (b) the single contest case. Each probability is based on 40,000 sample paths.

The second simulation involved only nine strategies, so as to get a detailed picture of evolutionary dynamics; we used a broad range of population sizes. In these simulations, we used the three stricter ways (S, MS, and CS) of assessing the probability that the population evolves to an ESS.

RESULTS

The First Simulation

The least strict (LS) probability that a population evolves to an ESS for a given population size and initial number of strategies is shown in Figure 2a for the IC case and in Figure 2b for the SC case. This probability overestimates the true

TABLE 1. Average quadratic component of the initial strategy distribution for populations that eventually became monomorphic and bimorphic in the first simulation.

Population size	Number of initial strategies	Infinite contest		Single contest	
		Monomorphic	Bimorphic	Monomorphic	Bimorphic
40	5	−0.023248***	0.151940***	0.008283*	−0.059983
	9	−0.027842***	0.131920***	0.003766	0.373060***
	17	−0.024453***	0.126450***	−0.001354	0.338880***
	33	−0.022756***	0.120310***	−0.009571*	0.336460***
80	5	−0.034309***	0.039100***	−0.005743*	0.093458***
	9	−0.034561***	0.054179***	−0.026140***	0.151920***
	17	−0.031023***	0.056764***	−0.032922***	0.166620***
	33	−0.029341***	0.050595***	−0.030679***	0.150940***
160	5	−0.031356***	0.020176***	−0.030737***	0.078193***
	9	−0.024965***	0.022263***	−0.034538***	0.063143***
	17	−0.026443***	0.023254***	−0.043126***	0.056468***
	33	−0.025286***	0.019420***	−0.042306***	0.067922***
320	5	−0.018236***	0.012306***	−0.019398***	0.015429***
	9	−0.019617***	0.007790***	−0.030996***	0.022809***
	17	−0.020495***	0.007501***	−0.032033***	0.024764***
	33	−0.019961***	0.008187***	−0.031044***	0.032127***
640	5	−0.011595***	0.006916***	−0.000890	−0.003941***
	9	−0.011602***	0.003952***	−0.020972***	0.004863**
	17	−0.013660***	0.003006***	−0.017417***	0.005163*
	33	−0.013084***	0.002801***	−0.014742**	0.007986**
1280	5	−0.005282***	0.003000***		
	9	−0.005061***	0.002143***		
	17	−0.005883***	0.001864***		
	33	−0.006321***	0.000932		

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

probability that the ESS evolves; the degree of overestimation declines as population size increases.

For the IC and SC cases, the LS probability depended on the population size. Smaller populations had higher probability of evolving the ESS; this probability declined substantially as population size increased, whatever the possible number of strategies in the initial population. For example, when there were 33 possible strategies in populations with no competitive stochasticity (IC), the probability was approximately 0.88 when the population size is 40, whereas it was approximately 0.09 when the population size was 1280. This effect of population size was not observed by Bergstrom and Godfrey Smith (1998).

The tendency to evolve an ESS depended on the number of strategies. For the IC case, the disparity of probabilities across different population sizes initially increased as the number of strategies increased. In contrast, in the SC case, there was no such initial increase as the number of strategies increased; we do not know why populations of size 640 with five possible strategies had a markedly lower probability of evolving the ESS as compared to similarly sized populations with more strategies (or as compared to smaller populations also having five strategies).

As expected, given the benefits of the ESS strategy in the face of uncertainty, the populations with SC generally had higher probabilities that an ESS evolves as compared to otherwise identical populations that have IC. This difference is a consequence of the increased stochasticity in the evolutionary dynamics caused by the random choice of opponents.

Table 1 shows the average quadratic component of the initial strategy distribution for the IC and SC cases. A negative value indicates that the distribution was concave-downward on average, while a positive value indicates the opposite. Analyses of the standard errors (as shown) indicate that eventual-ESS populations tended to start with concave-downward strategy distributions on average and eventual-non-ESS populations tended to start with the opposite. In addition, there was a tendency for the absolute magnitude of curvature to decrease as population size increases.

The Second Simulation

The results for the IC and SC cases are shown in Table 2. The results of the MS and CS ways of assessing the probability that the population evolves to an ESS indicate that this probability was at most approximately 0.5 and was usually distinctly smaller, especially for larger population sizes. This dependency on population size was also seen in Figure 2. We regard the MS and CS ways of assessing the probability to be most meaningful, given that the S way includes strategies quite distinct from the nominal ESS strategy (0.5). The CS way was used by Maynard Smith (1988) and Bergstrom and Godfrey Smith (1998; see above).

Table 3 shows the distribution of strategy pairs for those populations that became bimorphic. For both the IC and SC cases, the number of populations containing the ESS strategy (0.5) declined as the second strategy becomes more extreme (either less hawk or more hawk). This pattern is expected given the advantage in a nonequilibrium population of a strategy closer to the ESS strategy as compared to a strategy farther away (see above). Accordingly, we believe that the populations containing the ESS strategy would become

TABLE 2. The probability that an ESS evolved in the second simulation. For each population size (*N*), the number of fixations for each of the nine possible strategies is shown. S, MS, and CS denote the strict, more strict, and completely strict ways of assessing the probability. For the infinite contest case, each probability is based on 40,000 sample paths except $N = 2560$, which had 10,000. For the single contest case, each probability is based on 4000 sample paths except $N = 640$, which had 10,000, and $N = 1280$ and 2560, which each had 1000.

	Strategy (proportion hawk)									Probability		
N	0.000	0.125	0.250	0.375	0.500	0.625	0.750	0.875	1.000	S	MS	CS
Infinite contest												
30	3	1316	5504	7279	7437	6677	5107	2903	545	0.906	0.535	0.186
40	0	216	5135	7276	7713	6931	4982	1474	84	0.843	0.548	0.193
60	0	3	2994	7230	7993	6951	6787	184	2	0.804	0.554	0.200
80	0	0	699	7215	8129	6974	1741	16	0	0.619	0.558	0.203
120	0	0	26	6768	8332	6417	198	0	0	0.544	0.538	0.208
160	0	0	1	5403	8352	5316	17	0	0	0.477	0.477	0.209
240	0	0	0	1975	8459	2196	0	0	0	0.316	0.316	0.211
320	0	0	0	439	8185	695	0	0	0	0.233	0.233	0.205
480	0	0	0	10	7600	45	0	0	0	0.191	0.191	0.190
640	0	0	0	2	6982	3	0	0	0	0.175	0.175	0.175
1280	0	0	0	0	5904	0	0	0	0	0.148	0.148	0.148
2560	0	0	0	0	1328	0	0	0	0	0.133	0.133	0.133
Single contest												
30	1	96	347	525	651	709	664	573	434	0.891	0.471	0.163
40	0	38	322	573	696	756	670	552	376	0.902	0.494	0.174
60	0	1	214	547	733	810	705	512	192	0.881	0.522	0.183
80	0	0	83	555	760	816	732	427	37	0.843	0.533	0.190
120	0	0	7	491	784	855	685	120	0	0.736	0.533	0.196
160	0	0	0	286	811	871	555	22	0	0.636	0.492	0.203
240	0	0	0	64	812	858	264	0	0	0.499	0.433	0.203
320	0	0	0	7	825	860	79	0	0	0.443	0.423	0.206
480	0	0	0	0	675	776	4	0	0	0.364	0.363	0.169
640	0	0	0	0	1327	1565	1	0	0	0.289	0.289	0.133
1280	0	0	0	0	17	69	0	0	0	0.086	0.086	0.017
2560	0	0	0	0	1	10	0	0	0	0.011	0.011	0.011

TABLE 3. The distribution of strategy pairs for bimorphic populations in the second simulation when $N = 640$. For the infinite contest case, there were 33,013 bimorphic sample paths (of 40,000.) For the single contest case, there were 7107 bimorphic sample paths (of 10,000.) Strategies 1 and 2 are expressed as proportion of the hawk subtrait.

	Strategy 2								
Strategy 1	0.000	0.125	0.250	0.375	0.500	0.625	0.750	0.875	1.000
Infinite contest									
0.000	—	0	0	0	26	1825	2012	2094	2139
0.125		—	0	0	43	1929	1965	2074	2124
0.250			—	0	152	1912	2081	1995	1997
0.375				—	521	1883	1885	1881	1839
0.500					—	436	128	57	15
0.625						—	0	0	0
0.750							—	0	0
0.875								—	0
1.000									—
Single contest									
0.000	—	0	0	0	0	32	371	423	452
0.125		—	0	0	0	33	409	506	548
0.250			—	0	0	78	431	498	538
0.375				—	3	214	514	524	557
0.500					—	313	270	213	161
0.625						—	16	3	0
0.750							—	0	0
0.875								—	0
1.000									—

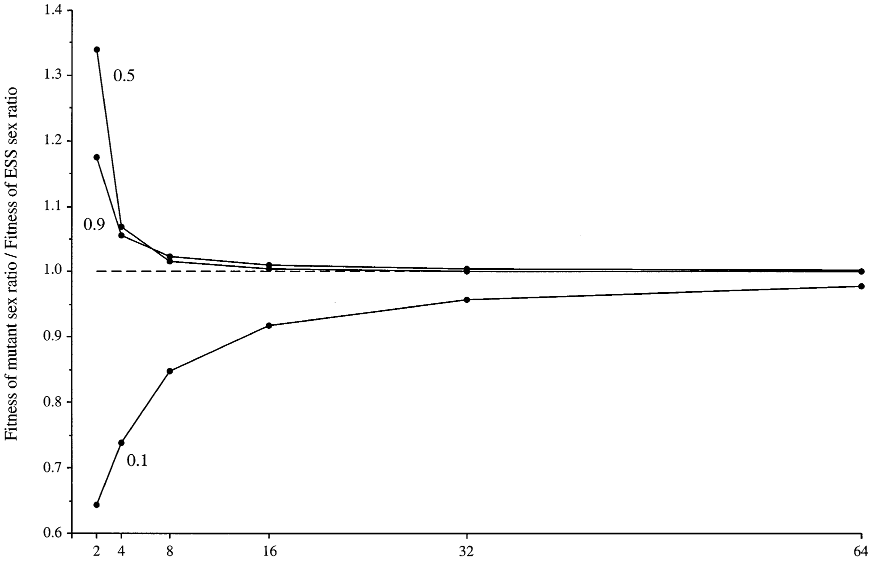

FIG. 3. Relative fitness of a mutant female producing a sex ratio of 0.1, 0.5, or 0.9 as a function of *N*, the total number of females contributing offspring to the local mating group. The other $(N - 1)/N$ females contributing offspring are assumed to each produce the ESS sex ratio. The inbreeding coefficient of the overall population (*F*) is equal to 0.01. A relative fitness of 1.0 is denoted by a dashed line.

monomorphic for that strategy given more time. The distribution of the number of bimorphic populations not involving the ESS strategy differed significantly from a uniform distribution (IC: $\chi^2 = 40.14$, df = 15, $P = 0.0004$; SC: $\chi^2 = 1013.15$, df = 15, $P = 0.0001$). We do not understand why such significant deviations occur or why they appear to have no pattern.

DISCUSSION

It is important to understand how our quantitative results are to be reconciled with those of Maynard Smith (1988) and Bergstrom and Godfrey Smith (1998), who reported that the probability that a population evolves to an ESS was approximately 0.70. More specifically, Bergstrom and Godfrey Smith showed that the probability decreased from approximately 0.75 for populations of size 12 to about 0.71 for larger populations up to size 4000 (see their figure 4). (We obtained similar results when starting populations with the special initial configuration they used, not shown.) This approximate constancy contrasts with the strong dependency on population size shown in Figure 2 and Table 2. This difference is readily explained as a consequence of our use of random initial strategy distributions because the effects of random initial sampling are both population-size dependent and appear to be long lasting in their effect on the eventual evolutionary outcome (see Table 1). However, Poethke's (1988, figure 7) analysis of the panmictic sex-ratio game appears to indicate a population-size dependent probability that an ESS evolves even though the two populations he simulated had the same initial distribution; to this extent, the typical effect of the initial distribution on the evolutionary outcome may depend on the game.

We believe that our simulations provide a more meaningful assessment of the overall probability that an ESS evolves than do the simulations of Maynard Smith and Bergstrom and Godfrey-Smith. Of course, the initial strategy distributions in nature are unknown; at the least, however, we think it reasonable to believe that initial strategy distributions that closely anticipate the ESS in having a high frequency of the ESS strategy and in being close to or at the evolutionarily stable state are not typical.

Our assessment of whether an ESS is likely to evolve has practical implications. The presence of an ESS is circumstantial evidence that natural selection has been the only important force affecting the evolution of the strategy (Orzack and Sober 1994). An ESS is locally optimal, as natural selection has eliminated all but one strategy that outperforms other strategies (Sigmund 1987; Liberman 1988). In contrast, the presence of an evolutionarily stable state is circumstantial evidence that both natural selection and genetic drift were important forces affecting the evolution of the population because frequencies of individual strategies are free to drift as long as the evolutionarily stable state is maintained. It is for this reason that an evolutionarily stable state does not support a claim of local optimality.

If an ESS were likely to evolve, it would imply that the assessment of individual strategy expression is of little or no importance because an evolutionarily stable state would likely be an ensemble of individuals each having the ESS strategy. Our results show that the probability that an ESS evolves is generally low, underscoring the importance of empirical assessment of the nature of strategy variation among individuals within natural populations. Unfortunately, such assessments are rare, as Orzack and Sober (1994) could find only two investigations containing such an assessment, despite an extensive search. Such assessments of whether an ESS or an evolutionarily stable state has evolved in a given instance can contribute to an ensemble test of adaptationism,

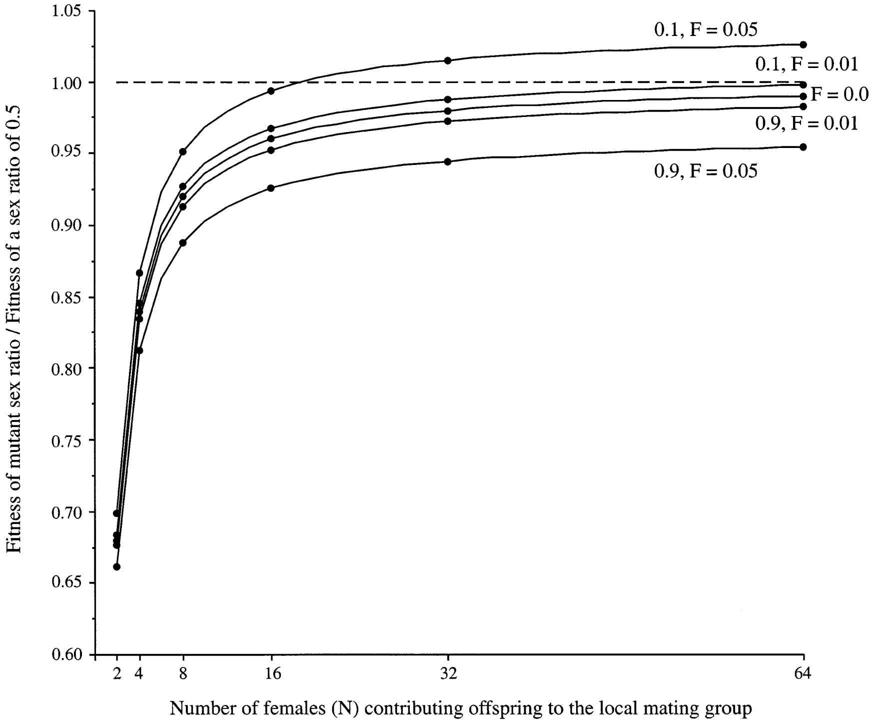

FIG. 4. Relative fitness of a mutant female producing a sex ratio of 0.1 or 0.9 as a function of N, the total number of females contributing offspring to the local mating group. The other $(N - 1)/N$ females contributing offspring are assumed to each produce a sex ratio of 0.5. The inbreeding coefficient of the overall population (F) is equal to 0.0, 0.01, or 0.05. When $F = 0.0$, the relative fitness depends only upon the magnitude of the deviation between the mutant sex ratio (0.1 or 0.9) and 0.5. A relative fitness of 1.0 is denoted by a dashed line.

since they provide evidence for adaptationism and pluralism, respectively (Orzack and Sober 1994). At present, one investigation (Brockmann et al. 1979) provided support for adaptationism and the other (Orzack et al. 1991) provided support for pluralism.

Beyond Fisher and Wright

In the degenerate strategic model analyzed here the strength of selection on strategies can increase as population size decreases. For example, as shown in Figure 1, the strength of the DPY effect is increased in smaller populations. A similar increase in the intensity of natural selection as population size decreases can also be observed in a nondegenerate model. For example, consider a model of local mate competition in which a finite number (N) of haplodiploid females produce offspring, all of which form a local mating group in which the offspring mate randomly. Standard reasoning (for further details, see Frank 1985; Herre 1985) indicates that the absolute fitness of a female that produces a brood with sex ratio r_a (proportion males) when, say, each of the other $N - 1$ females contributing offspring to the mating group produce broods with sex ratio r is proportional to

$$\frac{1}{2}r_a(1 - r_d) + \frac{1}{2}(1 - r_a)r_d\left(\frac{1 + 3F}{1 + F}\right), \tag{7}$$

where r_d is equal to $(1/N)r_a + [(N - 1)/N]r$ and F is the inbreeding coefficient for the entire population. The effect of population size on the intensity of natural selection can be illustrated in two different ways.

One is to assume that each of the $N - 1$ other females produce the ESS sex ratio for a group of size N,

$$r = \left(\frac{N - 1}{2N}\right)\left(\frac{1 + F}{1 + 2F}\right). \tag{8}$$

As shown in Figure 3, the intensity of selection affecting the single mutant that produces the non-ESS sex ratio decreases as the number of females (N) contributing offspring to the local mating group increases. For example, a sex ratio of 0.9 is more advantageous in a small population than it is in a large population (see also Verner 1965; Orzack et al. 1991, p. 593; and West and Herre 1998).

Another way is to assume that each of the $N - 1$ other females produce a sex ratio of 0.5 regardless of N. As shown in Figure 4, the intensity of selection affecting a single mutant that produces a different sex ratio changes as N increases. In fact, as population size increases the change in relative fitness for some mutant sex ratios (e.g., 0.1, $F = 0.05$) is such that the mutant is initially disadvantageous and then becomes advantageous. When $F \neq 0.0$, one can show that the intensity of selection for or against any given mutant sex ratio approaches a constant as N increases. When $F = 0.0$, the intensity of selection always decreases as N increases.

The strength of natural selection on a frequency-independent trait (as conventionally conceived) is independent of population size and thereby always increases relative to that of genetic drift when population size increases (Crow and Kimura 1970). Fisher (1930) and Wright (1932) made different assumptions about the size and structure of most populations but they shared an assumption that this relationship between population size and the relative strength of selection applied generally. One result is the common contrast between the Fisherian and Wrightian claims about nature. In the former, evolution typically occurs in large populations and accordingly, natural selection dominates the evolution of a trait; in the latter, evolution typically occurs in small and/or subdivided populations and accordingly, natural selection does not so dominate. The results we described involving frequency-dependent traits indicate that using population size as the basis for a generalization about the relative strength of natural selection may be mistaken. Because the absolute strength of natural selection on a frequency-dependent trait can decrease as population size increases, the strength of natural selection relative to genetic drift may be independent of population size or even decrease as population size increases. Further work is needed to elucidate this critical point (S. H. Orzack and W. G. S. Hines, unpubl. ms.). We note that as population size increased, the CS probability that an ESS evolved initially increased, was then approximately constant, and finally decreased (as shown in Table 2). One result is that this probability is larger for the smallest population as compared to the largest population. This overall pattern suggests that the strength of natural selection *relative* to genetic drift can be more or less constant or decrease as population size increases.

When pondering the fact that the relative strength of selection could be greater in smaller populations, it is worth remembering that no qualification as to the type of trait under consideration usually accompanies working definitions of the Fisherian and Wrightian claims. Most evolutionary biologists appear to use these claims in a way that is consistent with a belief that they apply to all traits. In this context, it is useful to remember the distinction between the organization of our study of nature and the organization of nature itself. A standard feature of population genetics textbooks (e.g., Crow and Kimura 1970; Li 1976) is that the constant viability model of natural selection is presented before any other model of natural selection. There are good reasons for this presentation, but it should not be taken to imply that this model applies generally to nature, as noted by Li (1967, p. 398), who refers to this model ''as the 'simplest' rather than the 'typical' or 'standard' case, because it is really unknown what is typical or standard in Nature, or if there is such a thing at all.'' This point deserves emphasis in the present context, especially given the ubiquity of the kind of interactive trait we have analyzed.

There is much irony at finding in Fisher (1930) both his general claim about the relationship between population size and the power of natural selection and his presentation of Düsing's (1883) argument as to why an even sex ratio can evolve; this argument is the ancestor of the strategic analyses we present, which suggest that Fisher's general claim is not correct.

It is intriguing to contemplate how different the recent history of evolutionary biology might have been if both Fisher and Wright had appreciated the importance of the kind of trait being considered when making their generalizations about evolution in natural populations.

Future Work

As noted above, we will seek to more explicitly characterize how population size affects the relative roles that natural selection and genetic drift have in the evolution of strategic traits. In addition, we will attempt to assess how more complicated genetic dynamics would affect the probability that an ESS evolves. Hines and Turelli (1997) have shown that the evolutionary dynamics of the haploid ESS model match the dynamics of the mean strategy in an additive multilocus, multiallele, sexual diploid model, regardless of the extent of linkage disequilibrium. Of course, what is at issue in the present context is the distribution of strategies underlying the mean strategy. Accordingly, Hines and Turelli's result is not sufficient grounds to believe that our overall conclusion about the tendency for an ESS to evolve applies to the polygenic case. Nonetheless, their analysis serves as a starting point for investigations of this question.

Finally, further work will also include elaboration of the connection between our results and those of related analyses of strategy evolution in finite dynamical systems in biology, economics, and evolutionary programming (A. Carter, pers. comm.; Fogel et al. 1997; Ficici and Pollack 2000; Stegeman and Rhode 2004; Taylor et al. 2004).

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