Will a Sexual Population Evolve to an Ess?

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WILL A SEXUAL POPULATION EVOLVE TO AN ESS?

Evolutionary game theory has been developed to help us to think about phenotypic evolution when the fitnesses of phenotypes are frequency dependent. It is based on the simplest possible assumption about heredity, namely that inheritance is asexual and exact. Most real populations of interest are sexual and diploid, and there must, therefore, be some doubts as to whether and to what extent the conclusions of game theory can be applied to them. This note takes a step toward resolving these doubts.

An ESS, or evolutionarily stable strategy, is a phenotype toward which the members of a population will evolve, given parthenogenetic (or haploid one-locus) inheritance (Maynard Smith and Price 1973). Will a sexual diploid population evolve to an ESS? If the ESS is a phenotype which can be produced by a homozygous diploid genotype, no difficulty arises; the ESS will be stable against invasion by any possible mutants. The difficulty arises if the ESS is a mixed one (i.e., if it involves a mixture of pure strategies) which can only be achieved by a genetically variable population.

Consider first a random-mating population in which only two pure strategies are possible. It will be convenient to refer to these as Hawk and Dove, but no restrictions are made as to the fitness values in the payoff matrix. The phenotype is determined by two alleles, 1 and 2, at a locus, as follows.

Genotype	11	12	22
Probability of Hawk phenotype	P_0	P_1	P_2

Lloyd (1977) has shown that if only two phenotypes exist, and there are two alleles at a locus, then a genetic polymorphism exists only if either (i) the fitnesses of the two phenotypes are equal (this corresponds to a mixed ESS; see Bishop and Cannings 1978), or (ii) the relative frequencies of the two alleles are the same in the two phenotypes.

What follows is simply an application of Lloyd's result to a particular case.

The frequency of Hawk is $F_1 = p^2P_0 + 2pqP_1 + q^2P_2$. Given F_1, the payoffs when playing Hawk and Dove, $E(H)$ and $E(D)$, respectively, can be calculated from the payoff matrix. The genotype fitnesses are then

$$W_{11} = P_0E(H) + (1 - P_0)E(D)$$

$$W_{12} = P_1E(H) + (1 - P_1)E(D)$$

$$W_{22} = P_2E(H) + (1 - P_2)E(D).$$

If $E(H) = E(D)$, (Lloyd's condition [i]), all three fitnesses are equal, and the population is at equilibrium. If the fitnesses are not equal, then elementary one-locus theory shows that the equilibrium frequency of allele 1 is

$$\hat{p} = \frac{P_1 - P_2}{2P_1 - P_0 - P_2}. \quad (1)$$

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At this equilibrium, it is easy to show that the frequencies of allele 1 in the Hawk and Dove phenotypes are equal, so Lloyd's condition (ii) is satisfied. Thus a polymorphic equilibrium can exist either at the ESS, or at $\hat{p}$.

Frequency $\hat{p}$ is an internal equilibrium only if $(P_1 - P_2)$ and $(P_1 - P_0)$ have the same sign; that is, if there is overdominance. (Note that the overdominance concerns the phenotype, which is frequency-independent, and not the frequency-dependent fitnesses.) Hence, if there is no overdominance, either (i) the population becomes genetically homozygous, or (ii) the population reaches the ESS.

Which of these occurs depends on P^*, the population frequency of Hawk at the ESS, which depends only on the fitness values in the payoff matrix. The various possibilities are illustrated in figure 1*A*. Either the population reaches the ESS, or, if the ESS lies outside the range of possible phenotypes, it becomes fixed for the genotype closest to the ESS.

If there is overdominance, the situation is more complex. The four possible cases are shown in figure 1*B*.

Case1.—P^* lies outside the genetically possible range, with the heterozygote lying closest to it. The only stable equilibrium is given by $\hat{p}$. This is not the ESS, but it can be shown that p is such as to maximize F_1, the frequency of Hawk, so that the population is as close to the ESS as its genetic system allows.

Case 2.—P^* lies within the genetically possible range. There are now two gene frequencies giving stable equilibria, both at the phenotypic ESS. The $\hat{p}$ equilibrium lies between them, and is unstable.

Case 3.—P^* still lies within the genetically possible range. Only one gene frequency gives the stable ESS equilibrium. This equilibrium is not globally stable, and there is a second stable equilibrium (not an ESS) for the fixation of one allele.

Case 4.—P^* is outside the genetically possible range, the heterozygote lying furthest from it. Fixation for either allele is stable, the basins of attraction being separated by an unstable equilibrium at $\hat{p}$.

These results can be summarized as follows.

i) If the ESS lies within the genetically possible range, then it will be stable. Unless there is overdominance, it will be the only stable state. If there is overdominance, there may be a second stable state, not at an ESS.

ii) If the ESS lies outside the genetically possible range, the population state closest to the ESS will be stable; it will usually be the only stable state (the only exception being overdominance case 4).

Hence for the two-strategy game, with two alleles at a locus, it is almost true to say that the population will evolve to an ESS if it can, and if it cannot it will approach the ESS as closely as the genetic system permits.

What of more complex games, or more complex genetic systems? For a given game, if the genetic system has more alleles or more loci and so permits a wider range of phenotypes, this will in general make it easier and not more difficult for the population to reach an ESS. Thus difficulties arise mainly with more complex games (i.e., more pure strategies are possible). First, it should be pointed out that, even with parthenogenetic inheritance, if there are more than two pure strategies, then the standard conditions for an ESS given by Maynard Smith and Price (1973)

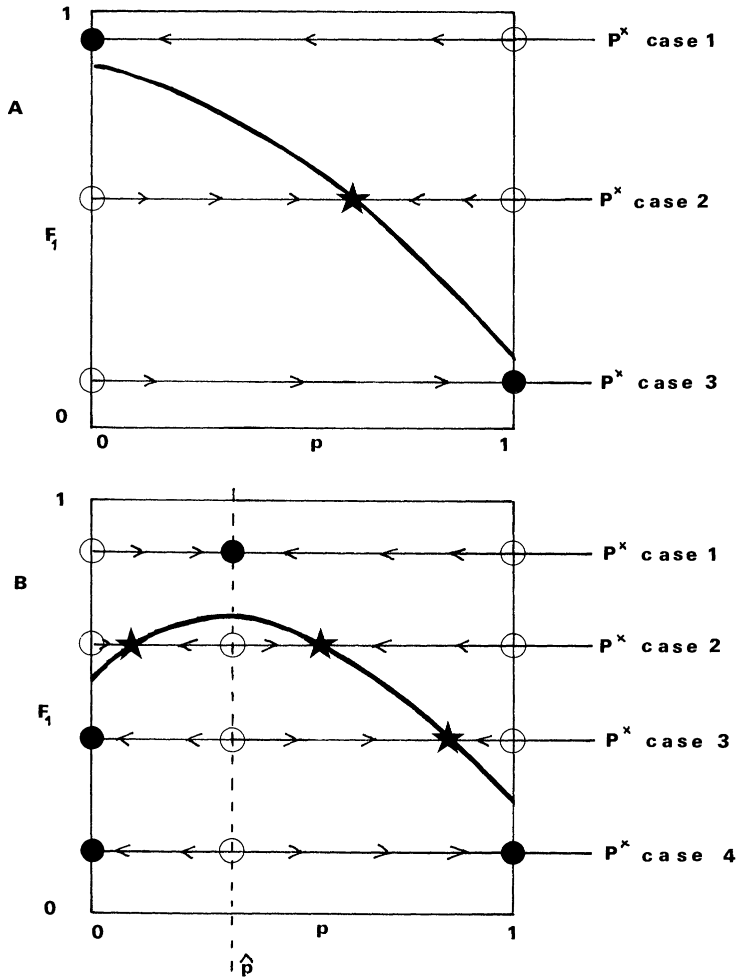

FIG. 1.—Equilibria for the two-strategy game with a diploid two-allele system. *A*, no overdominance; *B*, with overdominance. ○, unstable equilibria; •, stable equilibria; ★, ESS's. F_1 = frequency of Hawk in population; p = gene frequency; P^* = frequency of "Hawk" at ESS; $\hat{p}$ = gene frequency such that frequency is the same in the Hawk and Dove phenotypes. The bold line is a graph of F_1 against p.

guarantee the stability of a mixed ESS only if individuals adopting the mixed strategy can exist and breed true. Clearly, if this is the case, a mixed ESS would also be stable in a sexual population.

A difficulty only arises, therefore, if there is a complex game with a mixed ESS which can only be achieved by a genetically polymorphic population. Charlesworth, in an appendix to Lloyd (1977), has shown that if there are n phenotypes, and m alleles at a locus, then, provided $m \geqslant n$, a polymorphic equilibrium either requires that the phenotypic fitnesses are equal (i.e., an ESS), or requires a special condition on the gene frequencies, corresponding to condition (i) above but difficult to interpret. A similar conclusion has been reached for a more general model by Slatkin (1979). This encourages the hope that, if the genetic system is sufficiently complex relative to the range of possible phenotypes, the stable states will be ESS's. However, there will certainly be cases in which the ESS cannot be reached because of genetic constraints.

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