Group Selection among Alternative Evolutionarily Stable Strategies

ROBERT BOYD† AND PETER J. RICHERSON‡

† *Department of Anthropology, University of California, Los Angeles, CA 90024 and* ‡ *Institute of Ecology, University of California, Davis, CA 95616, U.S.A.*

Many important models of the evolution of social behavior have more than one evolutionarily stable strategy (ESS). Examples include co-ordination games, contests, mutualism, reciprocity, and sexual selection. Here we show that when there are multiple evolutionarily stable strategies, selection among groups can cause the spread of the strategy that has the lowest extinction rate or highest probability of contributing to the colonization of empty habitats, and that this may occur even when groups are usually very large, migration rates are substantial, and "extinction" entails only the disruption of the group and the dispersal of its members. The main requirements are: (1) individuals drawn from a single surviving group make up a sufficiently large fraction newly formed groups, and (2) the processes increasing the frequency of successful strategies *within* groups are strong compared to rate of migration among groups. The latter condition suggests that this form of group selection will be particularly important when behavioral variation is culturally acquired.

Introduction

Many types of social interactions have the property that once a behavioral strategy becomes sufficiently common, individuals using that strategy have higher payoff than individuals using alternative strategies. Such a strategy will increase under the influence of natural selection once its frequency exceeds a threshold. The simplest examples are co-ordination games in which fitness is frequency dependent but there is no conflict of interest among individuals (Sugden, 1985). The asymmetric Hawk–Dove game (Maynard Smith, 1982a) provides a good example. In this game, pairs of individuals contest for a resource that is possessed by one of them. It can be shown that both the "bourgeois" strategy (if possessor play hawk, if non-possessor play dove) and the "perverse bourgeois" strategy (if possessor play dove, if non-possessor play hawk) are evolutionarily stable. If one strategy becomes common, individuals using that strategy resolve contests without fighting, while individuals using the rare strategy will commonly engage in destructive conflict. Other kinds of social interaction involve a mix of conflict and co-operation. In the "battle of the sexes" game, individuals in two roles have a strong interest in co-ordinating their behavior but differ about which behavior is best. For example, both a male and female share an interest in one of them guarding the nest, but have very different interests in which one of them does the chore. Mutualistic interactions are represented by the so called "stag hunt" (Maynard Smith, 1982b; Boyd, 1988). Both

mutualistic and non-mutualistic behavior are evolutionarily stable, but there is a larger penalty for mistaken mutualism than for mistaken non-mutualistic behavior. Many models of reciprocity also have this payoff structure (Axelrod & Hamilton, 1981: Boyd, 1988).

Models with multiple stable equilibria are indeterminate in the sense that a knowledge of the fitness consequences of competing behaviors is not sufficient to predict which behavior will characterize a population. We can explain why a particular behavior persists once it is common, but unless we also know the initial state of the population, we can only predict that one of the equilibria will be reached. In many models, qualitatively different behaviors may be evolutionarily stable. In models of pairwise reciprocity, for example, behaviors ranging from non-co-operation to tit-for-tat may be evolutionarily stable (Axelrod & Hamilton, 1981; Sugden, 1985; Boyd, 1989). Since we rarely have knowledge of initial conditions, a wide range of observed behavior is consistent with an adaptive explanation.

Selection among groups provides a potential solution to this indeterminacy. In many models of social behavior, alternative stable equilibria have quite different levels of average fitness. For example, it is usually thought that the bourgeois strategy will lead to higher average fitness than the perverse bourgeois strategy because the latter would lead to an endless sequence of displacements. Similarly, in models of the evolution of reciprocity, populations in which reciprocating strategies like tit-for-tat are common may have much higher average fitness than stable equilibria entirely composed of non-co-operators (Axelrod & Hamilton, 1981). It is plausible that differences in average fitness might lead to differences in group persistence. Larger groups are less prone to extinction due to random demographic fluctuations or competition with other groups. Groups with harmonious social relations are more likely to persist than those with conflictual social relations. Either differences in average fitness or extinction rate make possible selection among groups.

Most existing analyses of group selection are not concerned with selection among alternative stable equilibria; rather they are about the evolution of altruistic behavior. By definition, altruistic individuals have lower fitness relative to non-altruists in their group. Thus, non-altruistic behavior is the only stable behavior in an isolated group. Group selection arises because groups with more altruists have higher average fitness or lower extinction rates. Wade (1978) distinguishes between intrademic models in which there is extensive migration among groups, and interdemic models in which groups are nearly isolated demes. Extensive theoretical analysis of inter-demic models (Eshel, 1972; Levin & Kilmer, 1974; Slatkin & Wade, 1978; Boorman & Levitt, 1980; Aoki, 1982; Crow & Aoki, 1982; Rogers, in press) suggests that interdemic group selection will lead to substantial levels of altruism only when groups are very small, migration rates are very low, and the intensity of selection among groups is high compared to the intensity of selection within groups.

There are a small number of models of group selection among alternative stable strategies. In models analyzed by Boorman & Levitt (1980), either co-operative or non-co-operative behavior is evolutionarily stable in an isolated subpopulation. However, in a stepping stone type model in which migration is limited to neighboring subpopulations, once co-operation becomes sufficiently common in a single deme,

then it can spread deterministically throughout the metapopulation as long as migration rates are neither too low or too high. If migration rates are too low, the group beneficial behavior cannot invade neighboring subpopulations; if they are too high, the group beneficial behavior cannot maintain a high frequency in the initial deme. Analogous results have been derived for the deterministic spread of a superior underdominant allele in a continuous spatial models (e.g. Barton, 1979). These models also require spatially limited migration, and the deterministic spread of the favored trait will be halted by any region with low migration rates or low equilibrium population size. Lande (1985) considers a model for the spread of an beneficial underdominant allele in an island type model in which migration occurs among all subpopulations. He assumes that migration rates are very low, but that there are frequent local extinctions. The extinction rate of a subpopulation does not depend on its genetic composition. For the most part, the favored allele spreads because subpopulations in which it is fixed are less invasible than populations in which the alternative allele is fixed, although local extinction accelerates the rate at which this process occurs. Because this process depends on drift for its direction, it requires that subpopulations be quite small, and is relatively slow.

In this paper, we consider a model in which interdemic group selection among alternative stable equilibria results from differential extinction of local subpopulations or differential contribution to the pool of individuals colonizing empty habitats. We show that this process will cause the spread of the behavior that maximizes group persistence as long as (1) selection *within* groups is sufficiently strong compared to migration, and (2) the probability that empty habitats are recolonized by a single subpopulation is sufficiently high. In contrast to interdemic group selection for altruism, there is no requirement that groups are always very small nor that migration rates are very low. Moreover, group "extinction" need only entail the disruption of the group and dispersal of its members to other habitats. In contrast to previous models of group selection among alternative stable strategies, migration need not be limited to neighboring groups and group selection can lead to rapid change.

We begin by presenting a simple model of selection among groups at alternative stable equilibria. We then derive approximate conditions for the spread of the group beneficial trait by group selection assuming (1) that selection among groups is much weaker than selection within groups, and (2) the number of groups is very large. This analysis generalizes work presented in Boyd & Richerson (1985: 230–235). Numerical simulations show that this approximate analysis provides a useful rule of thumb for the importance of group selection even when selection among groups is strong. These numerical results also suggest that group selection can lead to relatively rapid evolutionary change. Finally, we argue that this form of group selection will be particularly important when behavioral variation is culturally acquired rather than genetically.

The Model

The following simple model captures many of the salient features of games with multiple stable equilibria. Consider a metapopulation that is subdivided into a

number, n, subpopulations, or groups. Suppose that there are two behavioral strategies, one that is beneficial to the group (labeled B) and one that is deleterious to the group (labeled D). Let the frequency of B in subpopulation i at the beginning of a time period be q_i. Individuals interact socially only within groups. These interactions affect individual fitness, and the relative frequencies of the two strategies will change as a result of natural selection, or, alternatively, by learning (Dawkins, 1980; Harley, 1981; Maynard Smith, 1982a). Let q_i', the frequency of B after social interaction in group i, be given by

$$q_i' = q_i + f(q_i),\qquad(1)$$

where f gives the rate of increase of strategy B as a function of the frequency of B. We want to choose the form of f so as to capture the idea of multiple stable strategies with as few other restrictions as possible. To do this, we require:

(1) $f(0)$, $f(1) = 0$, and $f'(0)$, $f'(1) < 0$, where $f'(x) = df/dq_i$ evaluated at $q_i = x$. This assumption means that both B and D are evolutionarily stable in an isolated population because there is no tendency for q_i to change when it is 0 or 1 and slight displacements from 0 and 1 will tend back toward these values.

(2) $f'(x)$ has a only one local maxima in interval $0 < x < 1$. If this condition is satisfied, then (1) has a single unstable internal equilibrium, $\tilde{q}$ [i.e. $f(\tilde{q}) = 0$ and $f'(\tilde{q}) > 0$], and there are at most two stable equilibrium states in subpopulations linked by migration.

(3) $f'(x) > -1$. This assumption guarantees that subpopulations converge monotonically to stable equilibria even when they are linked by migration.

Figure 1 illustrates the shape of functions that satisfy these assumptions. When the initial frequency of B in an isolated population is greater than $\tilde{q}$, D decreases
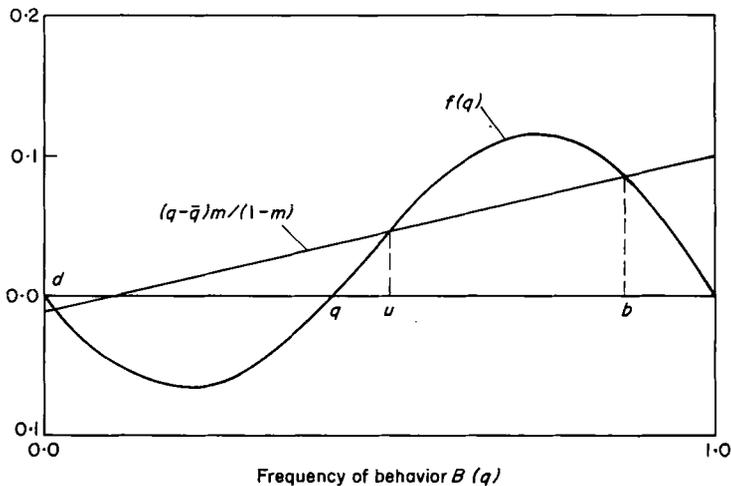

FIG. 1. This figure illustrates the assumed form of the function $f(q_i)$ and why there can be either one or three solutions to eqn (5). The straight line has slope $m/(1-m)$ and x-intercept $\hat{q}$. Solutions to (5) occur at the values of q_i at which this line intersects $f(q_i)$. As drawn there are three solutions. However, if m were increased there would only be one solution.

in frequency and eventually disappears. When the initial frequency of B is less than $\tilde{q}$, B decreases in frequency. This model applies to haploid population dynamics that are conventional in ESS analyses (Maynard Smith, 1982a; Zeeman, 1981), but also applies to other models that arise when there is cultural transmission (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985).

After social interaction, a fraction m of each subpopulation is replaced by individuals drawn randomly from the metapopulation. This means that the frequency of strategy B in subpopulation i after migration is:

$$q''_i = (1 - m)q'_i + m\bar{q}, \tag{2}$$

where $\bar{q}$ is the average frequency of B in the metapopulation before migration.

Next, suppose that occasionally a subpopulation is disrupted as a social unit— either through the death of its members, or their dispersal throughout the metapopulation. The probability that this occurs is a monotonically non-increasing function, $E(q_i)$, of the frequency of the group beneficial trait, B, in the subpopulation. Thus, selection among groups resulting from differential extinction will tend to increase the frequency of B in the metapopulation.

After an extinction, the empty habitat is recolonized by other subpopulations. Whether the increase in the frequency of B that is caused by extinction will persist depends on the distribution of the frequency of B among groups of colonists, which in turn depends on two factors: first, subpopulations in which B is common are assumed to have higher average fitness than subpopulations in which D is common. Thus, it is plausible that subpopulations in which B is common may generate more colonists. We will see that such differential proliferation also may lead to selection among groups. Second the distribution of the frequency of B among colonizing groups also depends on the way colonists are sampled from the metapopulation. Wade (1978) contrasts the migrant pool model in which colonists are drawn at random from the metapopulation with the propagule pool model in which colonists are drawn from a single randomly chosen subpopulation. In the migrant pool model, all groups of colonists will have similar mixes of B and D individuals unless such groups are very small, while in the propagule pool model the frequency of B among colonists may vary widely even if groups of colonists are very large. Experience with other group selection models (Wade, 1978; Lande, 1985) suggests that group selection is more potent with the propagule pool than the migrant pool model, and we will see that the present model has similar properties. To formalize the effects of both differential proliferational and the mode of sampling, let $H(x)$ be the probability that the frequency of B among colonizers is greater than some threshold value x.

Approximate Analysis

In this section, we derive approximate conditions under which the group beneficial variant, B, will spread to the whole metapopulation once it becomes common in a single subpopulation given two simplifying assumptions:

(1) extinctions are sufficiently rare, and subpopulations are large, and (2) the number of subpopulations is very large. We make these assumptions because they simplify the analysis, not because they are especially favorable to the action of group selection. To the contrary, increasing the size of subpopulations and reducing the strength of selection among groups extinctions should act to weaken selection among groups.

When extinctions are rare and subpopulations are large, three qualitatively different kinds of processes affecting the population act on different time scales. First, the within-group processes of selection and migration act on very short time scales. Second, on a longer time scale, differential extinction and proliferation may lead to selection among groups. Finally, on still longer time scales drift (and drift-like random processes in the case of cultural transmission) will cause subpopulations to shift from one equilibrium state to another. When there are many subpopulations, changes in the frequency of the beneficial type in a single subpopulation has only a small effect on its average frequency in the metapopulation.

If extinctions are very infrequent, the metapopulation can be assumed to be approximately at equilibrium under the influence of migration and selection each time an extinction occurs. Such approximate equilibria are of two types: either (1) all of the subpopulations are fixed for one or the other behavior, or (2) subpopulations are in one of two subpopulation equilibria, one at which B is relatively common, or one in which D is relatively more common. The equilibrium frequencies, $\hat{q}_i$, in each subpopulation must satisfy:

$$0 = f(\hat{q}_i) + \frac{m}{1-m}(\hat{q} - \hat{q}_i), \tag{3}$$

where $\hat{q}$ is the average equilibrium frequency in the metapopulation. For a given average frequency, the assumed form of f guarantees that this equation can have either one or three solutions (see Fig. 1). If there is only one solution, all subpopulations must have the same frequency, and therefore (3) becomes $f(\hat{q}_i) = 0$, which can only be satisfied if the frequency of B in all subpopulations is either zero or one.

Suppose that (3) has three solutions for some $\hat{q}$, and let the frequency of B at these subpopulation equilibria be d, u, and b such that $d < u < b$. Because the number of subpopulations is large, changes in the frequency of B in one subpopulation have only a small effect on the average frequency in the metapopulation, and therefore each subpopulation can be thought of as an island experiencing migration from a large continent. Then d and b can be thought of as stable island equilibria of such a continent-island model, and u the unstable intermediate equilibrium. A stable metapopulation equilibrium must consist of a fraction p of the subpopulations at b and $(1-p)$ at d, where $pb + (1-p)d = \hat{q}$. It is important to keep in mind that the subpopulation equilibrium frequencies depend on the average frequency of B in the metapopulation because of migration. As $\hat{q}$ increases, so do b and d, but u decreases. To emphasize this fact we will sometimes write b, d, and u as functions of p, the fraction of subpopulations in which B is common.

Intuitively, weak selection cannot maintain an island at a different frequency than the continent in the face of migration, and all islands will be alike. Once either

behavior becomes sufficiently common in the metapopulation, it is favored by selection, and one or the other behavior comes to dominate the metapopulation; no one island will be able to resist the effects of migration from the other islands. In contrast, strong selection can maintain an island at a different frequency than the metapopulation because the direction of selection depends on the local frequency of the two behaviors. If one behavior is common in some subpopulations, but not others, strong selection can act to counteract migration and preserve variation among subpopulations. We will argue below that other directional forces can have the same effect.

We can now derive approximate conditions for B to increase under the influence of group selection. Consider a metapopulation in which every subpopulation begins fixed for D, but then B reaches high frequency in a single subpopulation as a result of drift or environmental variation that affects the fitness of B (or some character that is genetically correlated with B). If group selection is to be important, B must stay common in the initial subpopulation long enough to increase by differential extinction. When extinctions are rare, this will only occur if there are three subpopulation equilibria when the average frequency of B in the metapopulation is zero. It follows from (3) that this will occur if

$$\max_{0<q<1} \{f(q)/q\} > m/(1-m). \tag{4}$$

This condition says that for there to be three approximate subpopulation equilibria, there must be some frequency at which the selection differential of B resulting from social interaction exceeds the effect of migration. When (4) is satisfied, the initial subpopulation can persist at a stable equilibrium $b(p)$ where p, the fraction of subpopulations at that equilibrium value, is $1/n$. In the rest of the subpopulations the frequency of B individuals, $d(p)$, is very low. This configuration will be maintained until the next extinction occurs.

Once a subpopulation at b arises through drift, selection among groups will increase the expected frequency of B in the metapopulation if

$$H[u(p)] > \frac{pE[b(p)]}{pE[b(p)] + (1-p)E[d(p)]}, \tag{5}$$

where initially $p = 1/n$. The right hand side gives the probability that a given extinction occurs in a b subpopulation; the left hand side gives the probability that a given extinction is recolonized by a propagule that will end up at the b equilibrium. Because the number of subpopulations is large, the extinction will cause only a small shift in the frequencies of B in all other subpopulations, and thus $\hat{q}$ will increase only a very small amount. Moreover, this will be true whether extinction involves the death of the individuals in the extinct subpopulation or merely their dispersal to the rest of the metapopulation. If the frequency of B among colonizers is greater than u, the newly colonized subpopulation will reach a stable equilibrium at which B is common, now $b(2/n)$, and the frequency of B in all of the other subpopulations will increase slightly to $b(2/n)$ and $d(2/n)$. Thus, as long as

extinctions are rare enough that subpopulations almost always return close to equilibrium between extinctions, the left hand side of (5) gives the relative birth rate of b subpopulations, and the right hand side the relative death rate of b subpopulations. If the birth rate is higher than the death rate, each extinction will, on the average cause B to increase.

It is instructive to consider the form that condition (5) takes in the special cases of the migrant and propagule pool models of colonization and assuming B is rare. In the migrant pool model, the frequency of B among colonizers is approximately d because B has this frequency in the overwhelming majority of subpopulations. Thus $H[u(1/n)] = 0$. When B is rare in the metapopulation, and colonizers are drawn one at a time from the pool of colonizers, there is no chance that the frequency of B among a large group of colonizers will be high enough to allow B to increase, even if subpopulations at $b(1/n)$ produce many more colonizers than subpopulations at $d(1/n)$. The propagule model is quite different in this regard. Suppose that b subpopulations produce k_b groups of colonizers and d subpopulations produce k_d groups of colonizers. The probability that B has frequency b in any particular group of colonizers, P, is:

$$P = \frac{pk_b}{pk_b + (1-p)k_d} > p. \tag{6}$$

There is a probability $(1-P)$ that it has frequency d. Since $b > u > d$, $H[u(p)] = P > p$. When colonists are drawn from a single subpopulation, subpopulations accurately reproduce themselves. In the propagule pool model, B will spread on average as long as (4) is satisfied and either subpopulations in which B is common produce more propagules than subpopulations in which D is common, or subpopulations in which B is common have lower extinction rates than subpopulations in which D is common.

The group beneficial trait is not *certain* to spread, however, even if (4) and (5) are satisfied. When there are only a few subpopulations in which B is common, they may be lost by chance extinction. The probability that B will actually spread to the entire metapopulation given that there is an initial subpopulation at b can be approximated using direct branching methods (Crow & Kimura, 1970). This probability is

$$1 - \frac{E[b(0)]}{1 - E[b(0)]} \frac{1 - E[d(0)]}{E[d(0)]H[u(0)]}. \tag{7}$$

Thus if increasing the frequency of B in a group has a strong effect on group persistence, the trait is very likely to spread once it reaches high frequency in a single group.

B will continue to spread under the influence of this form of group selection as long as all three subpopulation equilibria continue to exist, and (5) continues to be satisfied. For some forms of selection, there are three equilibria in subpopulations for all values of $\hat{q}$. However, for other forms of selection, only one equilibrium

exists above a threshold value of $\hat{q}$. When the average frequency of B in the subpopulation exceeds this threshold, B increases deterministically to fixation.

Numerical Results

The results derived so far depend on the assumption that extinction rates are very low. We performed a number of simulations to determine how sensitive the results are to this assumption. These simulations assume a haploid selection model in which the fitnesses of B individual is $W(B|q) = q + T(1-q)$ where the parameter T gives the incremental decrease in the fitness of B individual that results from increasing the frequency of D individuals. Similarly the fitness of D individuals is $W(D|q) = Sq + (1-q)$ where S measures the detrimental effect of B individuals. The effect of the frequency of B on subpopulation extinction is given by $E(q) = e_{min}q + e_{max}(1-q)$. Thus e_{min} is the extinction rate of a subpopulation made of all B individuals, and e_{max} is the extinction rate of a subpopulation composed of all D individuals. A fraction z of colonizers were drawn from a single randomly chosen subpopulation, and the rest from the metapopulation. Thus $z = 1$ corresponds to propagule pool model, and $z = 0$ corresponds to the migrant pool model.

In each of 535 cases, parameters were chosen at random as detailed below, and then 100 independent simulations were run. Initially, the frequency of B was set at $b(0)$ in one subpopulation, and zero in all the rest. Parameters were chosen as follows: T and S were uniformly distributed between zero and one. Then m was uniformly distributed between zero and an upper bound chosen such that there is a 50% chance of condition (4) being satisfied. z was uniform between one and one-half. The parameters e_{min} and e_{max} were chosen so that the expected fraction predicted by (7) was uniformly distributed between zero and one, and the minimum expected persistence time of a subpopulation was uniformly distributed between two and 20 generations. In all cases $n = 256$, and subpopulations were infinite in size so that no drift occurred.

These simulations indicate that conditions (4), (5), and (7) predict whether a group beneficial trait will spread even when extinctions are fairly common. B failed to spread in all 186 cases in which (4) was not satisfied. When (4) was satisfied, but not (5), B spread in five of 46 cases; in each of these, (5) was almost satisfied. In all of cases that (4) and (5) were satisfied, (7) provides a reasonable estimate of the probability that B will spread (see Fig. 2). In those cases in which B did successfully spread, the average time required for a given set of parameters ranged from 12 to 668 generations; the median time required across cases was 108·4 generations. There is a significant negative correlation between the calculated probability that B will spread, and the time that is required, given that it does spread.

Discussion

Most contemporary students of animal behavior agree that behaviors should be explained in terms of their benefit to individuals or their kin, not to the group as a whole. This belief is, for the most part, based on models which suggest that conditions
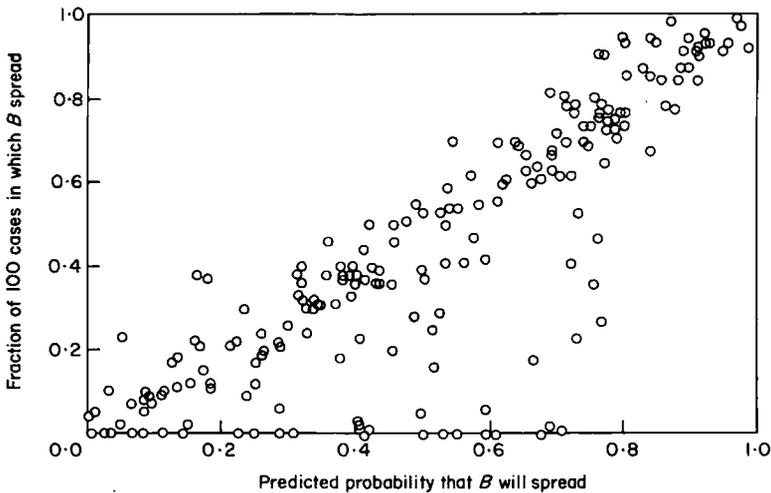
FIG. 2. This figure plots the fraction of 100 simulations reaching fixation for B in a metapopulation consisting of 256 infinite subpopulations as a function of the expected fraction predicted by (7). Parameters were picked as follows: T and S were uniformly distributed between zero and one. Then m was uniformly distributed between zero and an upper bound chosen such that there is a 50% chance of condition (1) being satisfied. z was uniform between one and one-half. e_{min} and e_{max} were chosen so that the expected fraction predicted by (7) was uniformly distributed between zero and one, and the minimum expected persistence time of a subpopulation was uniformly distributed between two and 20 generations. The theoretical model accounts for approximately 88·5% of the variance in the observed fraction reaching fixation.

under which interdemic group selection can lead to the evolution of altruism are extremely restrictive: groups must be very small, migration rates very low, and selection among groups quite strong, and these conditions are rarely satisfied in nature.

We think that this belief should be qualified. There is a great deal more to social behavior than altruism. Models of other types of social interaction have the property that many qualitatively different kinds of behavior can be evolutionarily stable. When this is the case, the individual costs and benefits of alternative behaviors can be used to explain why an observed behavior persists, but not why the observed behavior became common instead of some alternative evolutionarily stable behavior. The results presented in this paper suggest that under plausible conditions interdemic group selection can be a potent force leading to the spread of the evolutionarily stable behavior with highest probability of group persistence. Thus, if these conditions are met, it is reasonable to hypothesize that group benefit explains why a particular behavior is observed, rather than an alternative evolutionarily stable behavior.

Unlike traditional interdemic group selection process, this form of group selection can be a potent force even if groups are usually very large. For B to spread, first it must become common in an initial subpopulation. The rate at which this will occur through drift (or drift-like processes in the case of learning, Cavalli-Sforza & Feldman, 1981) will be slow for sizable groups (Lande, 1985). If (4) and (5) are

satisfied, however, and the frequency of B has a strong effect on persistence, this need only occur once. Thus, even if groups are usually large, occasional bottlenecks in some subpopulations could allow group selection to get started. Similarly, environmental variation in even a few subpopulations could provide the initial impetus for group selection.

It is sometimes argued that group selection resulting from differential extinction is inherently weak because extinctions are rare. In the form of group selection studied here, true extinction is not necessary. All that is required is the disruption of the group as a social unit and the dispersal of its members throughout the metapopulation. Such dispersal has much the same effect as extinction, because dispersing individuals have little chance of affecting the frequency of alternative behaviors in the future; in any one host subpopulation they will be too few to tip it from one equilibrium to another. Numerical results suggest that group selection can lead to rapid change even when social groups are disrupted on average less than every ten generations.

The model suggests that this form of group selection is very sensitive to the way in which new groups are formed. If new groups are mainly formed by individuals from a single pre-existing group, then the behavior with the lower rate of extinction or higher level of contribution to the pool of colonists can spread, even when it is rare in the metapopulation. In many primate species new groups are formed through the fissioning of existing groups. On the other hand, if new groups result from the association of individuals from many other groups, group selection cannot act to increase the frequency of rare strategies.

This form of group selection should be most important when the adaptive processes acting within groups are strong compared to migration. In traditional interdemic group selection models (Slatkin & Wade, 1978; Price, 1970; Boorman & Levitt, 1980), selection within groups acts to decrease between group variation for altruistic traits, and as a result group selection is important only if selection within groups is weak compared to drift. In contrast, when social interaction creates multiple stable ESSs, within group adaptive processes act to *maintain* among group variation. Given that per capita migration rates among neighboring groups will tend to increase as group size decreases (as the ratio of boundary length to group territory area increases), stronger selection (or learning) within groups will allow variation to be preserved among smaller groups. Since smaller groups are likely to have lower persistence, and higher rates of drift, stronger within group processes should lead to more rapid group selection.

This fact suggests that behaviors acquired by learning or cultural transmission are more likely to be group beneficial than genetically acquired behaviors. When there are overlapping generations, learning may maintain behavioral variation among subpopulations. Several authors have argued that learning and selection are similar processes (Harley, 1981; Dawkins, 1980; Boyd & Richerson, 1985). Instead of selection eliminating deleterious alleles, individuals reject behaviors that they find to be deleterious. If social behavior is partly shaped by the experience of interacting with older conspecifics, young individuals will tend to acquire behavior that conforms to the prevailing ESS. As a result the same behaviors will be ESSs

whether they are learned or genetically inherited. However, in many cases, it is likely that learning will lead to much more rapid adaptation than natural selection alone, and hence in more effective maintenance of subpopulation variation. The potential for rapid evolution also characterizes cultural transmission when learned variants are transmitted or when biases affect transmission (Boyd & Richerson, 1985). Drift-like effects can also be exaggerated under some schemes cultural transmission (Cavalli-Sforza & Feldman, 1981), and the exploration of the space of possible ESSs may be more thorough with cultural than genetic transmission. Thus, when social behavior leads to multiple stable ESSs, learning combined with social transmission, can maintain more variation among groups than natural selection for a given amount of migration. As a result, group selection should be stronger. Viewed from the within-group perspective, behavior will seem egoistic, but the egoistically enforced equilibra with the greatest group benefit will ultimately prevail.

REFERENCES

AOKI, K. (1982). *Evolution* **36**, 832–842.
AXELROD, R. & HAMILTON, W. D. (1981). *Science* **211**, 1390–1396.
BARTON, N. H. (1979). *Heredity* **43**, 341–359.
BOORMAN, S. & LEVITT, P. (1980). *The Genetics of Altruism*, New York: Academic Press.
BOYD, R. (1988). *Ethol Sociobiol.* **9**, 211–223.
BOYD, R. (1989). *J. theor. Biol.* **136**, 47–56.
BOYD, R. & RICHERSON, P. J. (1985). *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
CAVALLI-SFORZA, L. L. & FELDMAN, M. W. (1981). *Cultural Transmission and Evolution*. Princeton N.J.: Princeton University Press.
CROW, J. F. & AOKI, K. (1982). *Proc. natn. Acad. Sci. U.S.A.* **79**, 2628–2623.
CROW, J. F. & KIMURA, M. (1970). *Introduction to Population Genetics Theory*. New York: Harper and Row.
DAWKINS, R. (1980). In: *Sociobiology: Beyond Nature/Nurture* (Barlow, G. W. & Silverberg, J., eds) pp. 331–367. Boulder, CO: Westview.
ESHEL, I. (1972). *Theor. pop. Biol.* **3**, 258–277.
HARLEY, C. B. (1981). *J. theor. Biol.* **89**, 611–633.
LANDE, R. (1985). *Heredity* **54**, 323–332.
LEVIN, B. R. & KILMER, W. L. (1974). *Evolution* **28**, 527–545.
MAYNARD SMITH, J. (1982a). *Evolution and the Theory of Games*. London: Cambridge University Press.
MAYNARD SMITH, J. (1982b). In: *Current Problems in Sociobiology* (Kings College Sociobiology Group, eds) Cambridge: Cambridge University Press.
PRICE, P. G. (1970). *Nature, Lond.* **227**, 520–521.
ROGERS, A. (in press). *Am. Nat.*
SLATKIN, M. & WADE, M. (1978). *Proc. natn. Acad. Sci. U.S.A.* **75**, 3531–3534.
SUGDEN, R. (1985). *The Economics of Rights, Co-operation and Welfare*. Oxford: Basil Blackwell.
WADE, M. J. (1978). *Q. Rev. Biol.* **53**, 101–114.
ZEEMAN, E. C. (1981). *J. theor. Biol.* **89**, 249–270.