View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by The University of Utah: J. Willard Marriott Digital Library

Group Selection by Selective Emigration: The Effects of Migration and Kin Structure

Alan R. Rogers

The American Naturalist, Vol. 135, No. 3. (Mar., 1990), pp. 398-413.

Stable URL:
http://links.jstor.org/sici?sici=0003-0147%28199003%29135%3A3%3C398%3AGSBSET%3E2.0.CO%3B2-D

The American Naturalist is currently published by The University of Chicago Press.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/ucpress.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org
Fri Sep 28 10:50:38 2007

Vol. 135, No. 3 The American Naturalist March 1990

GROUP SELECTION BY SELECTIVE EMIGRATION: THE EFFECTS OF MIGRATION AND KIN STRUCTURE

ALAN R. ROGERS

Department of Anthropology, 102 Stewart Hall, University of Utah, Salt Lake City, Utah 84112

Submitted December 9, 1986; Revised August 20, 1987, and June 8, 1988; Accepted February 28, 1989

Natural selection operates on differences between local populations as well as on differences between individuals within them, but the importance of the between-group component is controversial. Since 1962, this controversy has focused on models of *selective extinction*, a mechanism that favors groups with a low probability of extinction. This paper is concerned with a different mechanism, that of *selective emigration*, in which the favored groups are those producing the most emigrants (Wright 1932; Uyenoyama 1979). I use the term *group selection* to refer to both mechanisms, although other uses for this term have been suggested (Maynard Smith 1976, 1982; Uyenoyama and Feldman 1980; Nunney 1985).

Most evolutionists doubt that any form of group selection can prevail against individual selection, except under unusual circumstances (Maynard Smith 1976). The seeds of this doubt were sown by Wright himself, who often emphasized that evolution by selective emigration requires

> a certain balance among its factors. There must be gene mutations, but an excessive rate gives an array of freaks, not evolution; there must be selection, but too severe a process destroys the field of variability, and thus the basis for further advance; prevalence of local inbreeding within a species has extremely important evolutionary consequences, but too close inbreeding leads merely to extinction. *A certain amount of crossbreeding is favorable, but not too much.* (Wright 1932, p. 38, italics added.)

Later theoretical work has shown that selective extinction can be important only if group sizes are small and the rates of migration between them low, in agreement with Wright's statements about selective emigration. It is often emphasized that, in many species, these conditions are met so rarely that group selection is unlikely to be important.

However, it is not clear that selective emigration requires the rate of crossbreeding, that is, migration between groups, to be low (Maynard Smith 1982). In the absence of migration, it is clear that there can be no selective emigration (Pollock 1983). On the other hand, selective emigration can operate when all individuals leave their local groups and mate at random within the population as a whole (Uyenoyama 1979; Wilson 1984). Wright apparently thought that selective

Am. Nat. 1990. Vol. 135, pp. 398–413.
© 1990 by The University of Chicago. 0003-0147/90/3503-0008$02.00. All rights reserved.

emigration works best at some intermediate level of migration, but he never published a detailed analysis justifying this point of view.

To my knowledge, there is only one detailed model bearing on this question (Harpending and Rogers 1987), and that model does not support Wright's point of view. Gilpin and Taylor (1988) have confirmed the results of that model but disagree with the conclusion that selective emigration is likely to be an important evolutionary force. The present paper extends and clarifies the results, using a related model, and reassesses the importance of selective emigration.

COMPONENTS OF SELECTION IN SUBDIVIDED POPULATIONS

In this paper, the bearers of an *altruistic* allele are selected against within local groups, but they enhance the mean fitness of their local group relative to other groups. (Thus, the bearer and not the allele itself is altruistic.) Altruistic effects are assumed to be distributed uniformly among group members, including the altruist himself. When the altruist's beneficial effect on himself outweighs the cost of altruism, the behavior is referred to as *weak altruism* (Wilson 1984) or *benevolence* (Nunney 1985). The unqualified term *altruism* is used indiscriminately for both the strong and the weak forms. The conditions under which altruism can evolve by selective emigration are precisely those under which selective emigration is stronger than individual selection within groups. Thus, although genetic models of altruism are usually motivated by an interest in the evolution of social behavior, they also serve to specify the circumstances under which selective emigration is an important evolutionary force.

Consider the evolution of an altruistic allele A in a large population subdivided into K local groups, between which some migration occurs. The order of events in the life cycle is

$$\text{reproduction} \rightarrow \text{density-dependent population regulation}$$
$$\rightarrow \text{migration} \rightarrow \text{selection} \rightarrow \text{reproduction}.$$

Individuals are referred to as *juveniles* before selection and as *adults* afterward. Let n_i and p_i denote, respectively, the size of the ith group and the frequency of A within it immediately after migration. The frequency of A in the population as a whole is

$$\bar{p} = \mathrm{E}\{p_i\} = \sum n_i p_i \Big/ \sum n_i .$$

Here and elsewhere the expectation operator, $\mathrm{E}\{\ \}$, refers to an average over groups, weighted by group size. Following Price (1970), the frequency of A in the following generation is written as

$$\bar{p}' = \mathrm{E}\{\overline{w}_i p_i'\},$$

where $\overline{w}_i$ is the mean fitness of group i relative to the mean fitness of the total population, and p_i' is the frequency of A among adults of the next generation who were born in i. Price's (1970, 1972) formulation of natural selection has often been used in studies of kin and group selection (Crow and Aoki 1982, 1984; Queller

1985; Wade 1985). It allows the effect of one generation of selection, $\Delta\bar{p} = \bar{p}' - \bar{p}$, to be expressed as a sum of between- and within-group components. As shown in the Appendix, this decomposition can be written as

$$\begin{aligned} \Delta\bar{p} &= (\mathrm{E}\{\bar{w}_i p_i\} - \bar{p}) + \mathrm{E}\{\bar{w}_i p_i (w_i^{(A)} - 1)\} \\ &= \Delta\bar{p}_{\mathrm{G}} + \Delta\bar{p}_{\mathrm{I}}, \end{aligned} \tag{1}$$

where the terms in the second line equal the corresponding terms in the first, and $w_i^{(A)}$ is the allelic fitness of A within group i, relative to the mean group fitness, $\bar{w}_i$. I refer to $\Delta\bar{p}_{\mathrm{G}}$ and $\Delta\bar{p}_{\mathrm{I}}$ as the group and individual components of selection, respectively.

Selective Emigration

Harpending and I used a model (Harpending and Rogers 1987) of a haploid population in which births, deaths, and migration occur in continuous time. The model is modified here by assuming generations to be discrete and by dealing with diploids as well as haploids. The average juvenile in group i produces, as an adult, $\alpha(1 + gp_i)$ emigrants, where p_i is the frequency of the altruistic allele among juveniles, α is the number of emigrants produced per individual in a purely selfish group, and $\alpha(1 + g)$ is the corresponding number for a purely altruistic group. A fraction m of the juveniles in each group are immigrants, and the rest are natives. Immigrants are not necessarily drawn at random from the pool of emigrants and may come preferentially from nearby groups. However, the range of possible population structures is limited by the assumption that each emigrant has an equal chance of being accepted into a group.

Because of density-dependent population regulation, the average juvenile in group i produces $1 - m$ nonemigrant offspring and $\alpha(1 + gp_i)$ emigrant offspring, of which the fraction $v^{(\bar{p})}$ are accepted as immigrants into another group. Thus, the average fitness of juveniles in the ith group is

$$\bar{w}_i = (1 - m) + \alpha(1 + gp_i)v^{(\bar{p})}.$$

Since emigrants are accepted into groups at a rate m but are produced at a rate $\alpha(1 + g\bar{p})$, it follows that the average fitness of emigrants is

$$v^{(\bar{p})} = m/\alpha(1 + g\bar{p}),$$

and, after rearranging,

$$\bar{w}_i = 1 + b^{(\bar{p})}(p_i - \bar{p}),$$

where

$$b^{(\bar{p})} = \alpha g v^{(\bar{p})} = mg/(1 + g\bar{p})$$

is the benefit per altruist, expressed in units of fitness rather than excess emigration. Note that this benefit is an increasing function of the immigration rate and a decreasing function of the mean frequency of altruists. Note also that, because of the assumption that group sizes do not change, $\mathrm{E}\{\bar{w}_i\} = 1$. Thus, absolute fitnesses and fitnesses relative to the mean are equivalent.

The group component of selection is, by equation (1),

$$\begin{aligned}\Delta\bar{p}_G &= E\{p_i[1 + b^{(\bar{p})}(p_i - \bar{p})]\} - \bar{p} \\ &= b^{(\bar{p})}V_B,\end{aligned}$$

where $V_B = E\{p_i^2\} - \bar{p}^2$ is the variance of group allele frequencies after migration but before selection. This result holds for diploids as well as for haploids.

Individual Selection

Individual selection may operate through either differential mortality or differential fertility. In the latter case, it is necessary to assume that the fitnesses of mated pairs are the products of the individual fitnesses of the two mates. For diploids, assume that the fitnesses of genotypes AA, Aa, and aa are in the ratios $1 - 2c$ to $1 - c$ to 1, where c is the coefficient of selection against altruists within groups. This implies that the genic fitnesses of A and a, relative to the mean group fitness, are

$$w_i^{(A)} = \frac{1 - c(p_i + 1)}{1 - 2cp_i} \quad \text{and} \quad w_i^{(A)} = \frac{1 - cp_i}{1 - 2cp_i}.$$

Equation (1) now shows that the individual component of selection is

$$\begin{aligned}\Delta\bar{p}_I &= E\{\bar{w}_i p_i(w_i^{(A)} - 1)\} \\ &\approx -cE\{\bar{w}_i p_i(1 - p_i)\} \\ &\approx -cV_W,\end{aligned}$$

provided that individual selection and group selection are both weak. Note that V_W refers not to the variance of individuals within groups but to the genic variance within groups, $E\{p_i(1 - p_i)\}$. For haploids, the same formula is obtained, using the same approximations, if the local fitness of A relative to a is $1 - c$.

Combined Individual and Group Selection

The change in allele frequency due to both components of selection is

$$\Delta\bar{p} = \Delta\bar{p}_G + \Delta\bar{p}_I = b^{(\bar{p})}V_B - cV_W.$$

It can be shown that $V_B + V_W = \bar{p}(1 - \bar{p})$ (Wahlund 1975). Hence,

$$\Delta\bar{p} = \bar{p}(1 - \bar{p})[b^{(\bar{p})}F_{ST} - c(1 - F_{ST})], \tag{2}$$

where $F_{ST} = V_B/\bar{p}(1 - \bar{p})$ is one of Wright's (1951) fixation indices. The altruistic allele is favored by selection when the ratio of between- to within-group variance exceeds the ratio of cost to benefit, that is, when

$$c/b^{(\bar{p})} < G, \tag{3}$$

where $G = F_{ST}/(1 - F_{ST})$.

Inequalities of the same form as inequality (3) also hold for other models of group selection (e.g., Aoki 1982, eq. 7; Crow and Aoki 1982, eq. 11; Kimura 1983). The novelty in inequality (3) is the frequency dependence of $b^{(\bar{p})}$, the

group-selection effect. At equilibrium, inequality (3) becomes an equality, and $\hat{p} = Gm/c - 1/g$. No comparable equilibria exist under kin selection or selective extinction. Unless g is large, however, the dependence of $\Delta\bar{p}$ on $\bar{p}$ is weak, as is the tendency to return to this equilibrium.

MIGRATION AND GENETIC POPULATION STRUCTURE

A Standard of Comparison: The High-Migration Limit

The "high-migration limit" is Slatkin's (1981) term for the pattern of migration in which local groups are formed anew each generation by individuals drawn at random from the total population. This concept is useful as a standard against which other patterns of migration can be compared. It can be shown (Hamilton 1975; Wilson 1984) that at the high-migration limit, inequality (3) is approximately equivalent to $g/c > 2n$, ignoring terms of order $(2n)^{-2}$, where n is the average group size. This implies that each altruistic gene must enhance its own fitness by an amount exceeding the cost of altruism. Thus, only weak altruism (Wilson 1984) or benevolence (Nunney 1985) can evolve at the high-migration limit. It is of interest to ask how this conclusion is modified by more-realistic patterns of migration. To this end, let us define a quantity Ω, which will measure the extent to which selective emigration is facilitated by particular patterns of migration.

When selective emigration (g) is weak, inequality (3) is approximately

$$g/c > 2n/\Omega, \tag{4}$$

where $\Omega = 2nmG$. At the high-migration limit, $\Omega = 1$, and only weak altruism can evolve. When $\Omega > 1$, the opportunity for selective emigration is enhanced and stronger forms of altruism can evolve. By comparison, altruism between full sibs can evolve by kin selection when $b/c > 2$. With the same costs and benefits, therefore, selective emigration is as strong as kin selection between full sibs when $\Omega \geq n$, but it is at an n-fold disadvantage when $\Omega = 1$. To what extent is this disadvantage ameliorated by particular forms of migration?

The Neutral Approximation

The dynamic behavior of F_{ST}, and therefore Ω, depends not only on selection, but also on group sizes and the pattern of migration among them. If successful emigrants settle in nearby groups, distant groups will be relatively isolated and Ω relatively large. A comprehensive analysis, dealing with all these effects, has been achieved only for the simplest migration patterns (Uyenoyama 1979; Harpending and Rogers 1987). To deal with greater complexity, we must resort to approximations and computer simulation. One tactic is to approximate Ω by its equilibrium value under the effects of migration and drift alone, as seems reasonable when selection is weak. This neutral approximation was suggested by Wright (1945) and is often used (Levitt 1975; Crow and Aoki 1984). In at least one model of selective emigration, it turns out to be surprisingly accurate (Harpending and Rogers 1987).

For particular migration patterns, the neutral approximation for Ω can be obtained from an earlier model (Rogers and Harpending 1986). Substituting equa-

tion (7) of that model into inequality (4) produces

$$\Omega \approx m(K - 1)/2m_e K, \tag{5}$$

where m_e is the *effective migration rate*, a function of the eigenvalues of the migration matrix. The migration pattern is constrained only by the assumptions that a gene from any group can eventually reach any other, that some individuals breed without emigrating, and that the number emigrating from group i to group j equals that from j to i. Relation (5) shows that Ω is approximately independent of n and thus measures only the effect of migration on the opportunity for selective emigration. This formula will be used to compare the effects of several canonical patterns of migration, which represent extreme cases of isolation by distance and of uniform migration.

Perhaps the simplest model of migration is Wright's (1943) "island model," in which groups are of equal size and a fraction m of each one contains immigrants drawn from the population as a whole. Under this model, $m_e = m - m^2/2$, as is shown in the Appendix. Thus, $\Omega \approx (K - 1)/(2 - m)K$, an increasing function of m. This agrees with the earlier finding (Harpending and Rogers 1987) that selective emigration is facilitated by mobility, not by the isolation of local groups.

It also holds for other models of migration, including the "circular stepping-stone model" and the "toroidal stepping-stone model." In these models, as in most natural populations, immigrants to each group derive mainly from nearby groups rather than being drawn at random from the population at large. The circular model has K groups evenly spaced around a circle, each receiving immigrants at equal rates from its two nearest neighbors but receiving none from more-distant groups. The toroidal model has K groups evenly spaced on a $K^{1/2} \times K^{1/2}$ rectangular lattice covering the surface of a torus (a doughnut-shaped surface), with each group receiving immigrants at equal rates from its four nearest neighbors on the lattice. The two models exhibit the effects of isolation by distance in one and two dimensions, respectively. Both models are classics within population genetics (Carmelli and Cavalli-Sforza 1976; Maruyama 1977; Crow and Aoki 1984).

Values of Ω implied by these models under the neutral approximation are presented in table 1. In all models, Ω increases with the immigration rate (m) (in agreement with Harpending and Rogers 1987, but not with conventional wisdom). It is also facilitated by isolation by distance, as is indicated by the increasing values of Ω as one moves from island to torus to circle and from low to high values of K. Except for the circular model, these effects are surprisingly weak. Over the entire range of parameters considered, both the island and toroidal models imply that Ω differs from unity—its value at the high-migration limit—by no more than a factor of two. Thus, the population structures represented by these two models have very little effect on opportunities for evolution by selective emigration. The large values for the circular model show that genetic differentiation at equilibrium is much larger when the isolation by distance is one-dimensional rather than two-dimensional, in agreement with Crow and Aoki (1984). The relevance of this finding is discussed below.

These theoretical results suggest that Ω will be fairly close to unity except in

TABLE 1

NEUTRAL APPROXIMATION: THE VALUE OF Ω EXPECTED AT EQUILIBRIUM IN THE ABSENCE OF SELECTION UNDER THREE MODELS OF MIGRATION

Migration Model	K	Ω: Theory		
		$m = 0.2$	$m = 0.5$	$m = 0.8$
Island	16	0.5	0.6	0.8
	64	0.5	0.7	0.8
	100	0.6	0.7	0.8
	1,024	0.6	0.7	0.8
	10,000	0.6	0.7	0.8
Torus	16	0.6	0.6	0.8
	64	0.8	0.9	1.0
	100	0.8	1.0	1.0
	1,024	1.2	1.2	1.4
	10,000	1.6	1.6	1.6
Circle	16	1.4	1.5	1.8
	64	5.4	5.5	5.8
	100	8.4	8.5	8.8
	1,024	85.4	85.5	85.8
	10,000	833.4	833.6	833.8

NOTE.—The method of calculation is given in the Appendix. K, Number of colonies; m, immigration rate.

one-dimensional habitats, and this suggestion is supported by table 2, which presents estimates obtained from several human populations. The column labeled "genetics" is computed from estimates of F_{ST} obtained from (presumably) neutral genetic markers, using inequality (4). F_{ST} varies according to the stage of the life cycle at which individuals are censused (Long 1986) and may be twice as high before migration as after (Rogers and Harpending 1986). Here, the value after migration is appropriate, but many published estimates refer to samples of mixed ages. The bias introduced is not appreciable, however, if only order-of-magnitude estimates are required. The estimates of Ω in table 2 are, with one exception, fairly close to unity, the value expected at the high-migration limit. The large value for the polar population is interesting because that population is a circular array of settlements around the shore of the Arctic Ocean and is thus described fairly well by the circular stepping-stone model. Thus, data from human populations are consistent with the equilibrium values in table 1.

However, these results are of interest only to the extent that equilibria reached under neutral evolution are relevant to selective emigration. When the process converges very slowly toward this equilibrium, the equilibrium may be irrelevant. Since convergence is geometric for this process, its rate can be measured by the *half-life*, the number of generations required to get halfway from an arbitrary initial value to the equilibrium. The half-life values in table 3 were calculated using the neutral approximation (described in Rogers and Harpending 1986). These values show that the large values of Ω in table 1 correspond to equilibria that are approached extremely slowly. Presumably, the same is true of the polar population in table 2. Thus, the neutral approximation probably tells us little about the effect of the circular stepping-stone model of migration on selective emigration.

TABLE 2

GENETIC AND DEMOGRAPHIC PARAMETERS FOR SEVERAL HUMAN POPULATIONS

POPULATION	n	K	m	Ω Genetics	Ω Migration
!Kung	140	6	0.386	0.8	0.6
Bedik	113	6	0.273	0.7	0.5
Makiritare	88	6	0.087	—	1.1
Oxford	133	8	0.072	—	0.5
!Kung	125	9	0.444	—	0.8
Papago	189	10	0.261	2.3	0.8
Åland*	607	11	0.125	—	1.2
Gainj	34	11	0.316	1.5	1.5
Polar	7,076	11	0.055	70.8	2.8
Åland	581	12	0.179	2.3	1.2
Gidra	50	13	0.142	—	0.9
Bougainville	54	14	0.148	—	1.5
Bundi	114	16	0.364	0.7	0.7

NOTE.—Tabulated are mean group size (n), number of groups (K), mean immigration rate (m), and Ω, which is estimated both from genetic data using equation (4) and from migration data using equation (5). Sources for all data are cited in Rogers and Harpending 1986, except for additional data on the Gainj population (Wood 1986) and all the data on the Polar (Rychkov and Sheremet'eva 1980).

* Includes only individuals born before 1900.

TABLE 3

THE HALF-LIFE OF CONVERGENCE

MIGRATION MODEL	K	HALF-LIFE $m = 0.2$	$m = 0.5$	$m = 0.8$
Island	—	1.6	0.5	0.2
Torus	16	3.1	1.0	0.4
	64	11.0	3.9	2.0
	100	17.0	6.0	3.1
	1,024	170.7	61.4	32.5
	10,000	1,663.5	599.5	317.6
Circle	16	22.6	8.9	5.5
	64	359.7	143.8	89.8
	100	878.0	351.1	219.4
	1,024	92,053.7	36,821.2	23,013.0
	10,000	8.8×10^6	3.5×10^6	2.2×10^6

NOTE.—The half-life of convergence is the expected number of generations until Ω has converged half the way from any arbitrary starting value to its equilibrium value. In the island model, the speed of convergence does not depend on K, the number of groups; m, immigration rate.

Computer Simulations

So far, the effect of selection on Ω has been ignored, and a series of computer simulations was performed to evaluate this approximation for both the island model and the circular stepping-stone model of migration. Both models had to be modified somewhat in order to satisfy the present model's requirement that all emigrants have equal probability of acceptance into a group. In K groups, each

TABLE 4

SIMULATED VALUES OF Ω

Migration Model	c	g	K	Ω: Simulation $m = 0.2$	$m = 0.5$	$m = 0.8$
Island	0.0	0	16	0.6	0.7	0.8
			64	0.6	0.7	0.9
			100	0.6	0.7	0.9
Circle			16	1.7	1.7	2.3
			64	8.7	6.1	6.3
			100	9.2	9.6	11.5
Island	0.1	2	16	0.5	0.7	0.9
			64	0.5	0.7	0.9
			100	0.5	0.7	0.9
Circle			16	0.6	0.8	1.1
			64	0.6	0.9	1.5
			100	0.5	0.9	1.7

NOTE.—Each value of Ω is an average over the last 100 generations of each of 10 replicates, weighted by $\bar{p}(1 - \bar{p})$, and excluding those for which $\bar{p} < 0.05$ or $\bar{p} > 0.95$. c is the coefficient of selection against altruists within groups; g, the coefficient of selective emigration; K, the number of groups; m, immigration rate. In all runs, $n = 10$ individuals.

with n haploid individuals, and with immigration rate m, there is room for Knm immigrants, of which the ith group produces a fraction $(1 + gp_i)/K(1 + g\bar{p})$. The bias here toward groups with high p_i is the effect of selective emigration. Each emigrant drawn from the ith group is an altruist with independent probability p_i', where $p_i' = p_i w_i^{(A)}$ is the frequency of altruists after individual selection. The emigrants from each group are initially stored separately in an array.

A modified version of circular stepping-stone migration was simulated as follows. Each emigrant in turn searches around the circle for a group with a vacancy—one whose quota of immigrants is not yet filled—and then moves to fill it. In the first generation, the first emigrant from each group searches clockwise around the circle. Successive emigrants from a given group search in alternating directions. The process begins with the first emigrant from the first group, proceeds to the first from group two, and so forth until the array of emigrants is exhausted.

The standard version of the island model assumes that each immigrant is equally likely to come from any group, which precludes selective emigration. In simulations, the model was modified as follows. Each emigrant is first assigned a random location on the circle and then allowed to search for a vacancy using the stepping-stone algorithm described above. The pseudorandom numbers used in these simulations were generated with the generalized feedback-shift-register algorithm (Lewis and Payne 1973).

Each simulation comprises 10 independent replicate populations. Each generation, F_{ST} is calculated for each replicate in which $0.05 \leq \bar{p} \leq 0.95$. The values of Ω reported in table 4 are based on averages of the last 100 generations of these F_{ST} values, weighted by $\bar{p}(1 - \bar{p})$. The duration of each simulation, expressed in half-

TABLE 5

DURATION OF EACH SIMULATION EXPRESSED IN HALF-LIVES

Migration Model	c	g	K	Half-Lives Simulated $m = 0.2$	$m = 0.5$	$m = 0.8$
Island	0.0	0	16	128.8	400.0	928.8
			64	128.8	400.0	928.8
			100	128.8	400.0	928.8
Circle			16	8.9	22.4	36.3
			64	4.2	4.2	4.0
			100	4.0	4.0	4.1
Island	0.1	2	16	78.6	400.0	928.8
			64	128.8	400.0	928.8
			100	126.2	400.0	928.8
Circle			16	8.9	22.4	36.3
			64	1.4	4.2	4.0
			100	0.6	4.0	2.1

NOTE.—c is the coefficient of selection against altruists within groups; g, the coefficient of selective emigration; K, the number of groups; m, immigration rate. In all runs, $n = 10$ individuals.

lives, is shown in table 3. I tried to run each simulation for the larger of 200 generations or four half-lives in order to allow time for the system to reach the neighborhood of its equilibrium. In several cases, however, the runs ended much earlier because one of the alleles became fixed. Even these runs may be close to equilibrium, however, because selection seems to speed convergence.

Table 5 presents results both for neutral evolution ($c = g = 0$) and for strong selection ($c = 0.1$, $g = 2$). The neutral runs are in close agreement with the theoretical values in table 1, justifying some confidence in both the theory and the computer program. The simulations verify the pattern of Ω increasing as m increases, as K increases, and as one proceeds from island to circle. However, in the runs with selection, Ω is much smaller than predicted by the neutral theory and never exceeds unity, its value at the high-migration limit, by even a factor of two. Thus, under strong selection, selective emigration is not facilitated by even extreme forms of isolation by distance.

The homogeneity of these estimates of Ω is truly remarkable. The conditions considered here span the range from no isolation by distance to extreme isolation by distance, from low rates of migration to high rates, and from few local groups to many; and in all of these cases, an altruistic allele is favored only if g/c exceeds a number that is within a factor of two of $2n$.

Kin-Structured Migration

Another factor that may facilitate selective emigration is *kin-structured migration* (KSM), which occurs when relatives tend to migrate together rather than independently (Fix 1978, 1985).

I have shown (Rogers 1987, 1988*a*), using a neutral model, that under KSM, $G \approx G^{(\text{No KSM})} \times (1 + 2m_e\alpha_M)$, where $G^{(\text{No KSM})}$ is the value G would have in the absence of kin structure, and α_M measures the extent to which migration is kin-

structured (this α follows the notation in Rogers 1988*a*; it should not be confused with the parameter α used above, which follows the notation in Harpending and Rogers 1987). Substituting this result into inequality (4) shows that kin-structured migration has the same effect as increasing Ω by a factor of $1 + 2m_e\alpha_M$. The magnitude of α_M depends on the size and constitution of the groups of relatives that migrate together. It has been estimated in only one human population, where it is near zero (Rogers 1988*b*). It seems likely, however, that α_M is often larger, perhaps as large as three (Rogers 1987, 1988*a*). Thus, in a population with high mobility ($m_e = 0.5$), kin-structured migration might triple the value of Ω. An increase of this magnitude, however, is still small compared with the n-fold disadvantage of selective emigration. Even with strongly kin-structured migration, evolution of altruism by selective emigration requires that g/c exceed a number of order n.

DISCUSSION

Where Will Selective Emigration Be Most Important?

As we have seen, selective emigration is facilitated by mobility rather than by isolation of local groups. This is somewhat counterintuitive. All forms of group selection depend for their action on the between-group component of genetic variance, and this component of variance is diminished by migration. Thus, it is often argued that group selection is most important where mobility between local groups is low (Wright 1932, 1945; Maynard Smith 1964, 1976; Williams 1966; Lewontin 1970; Eshel 1972; Aoki 1982; Crow and Aoki 1982; Wade 1982; Arnold and Fristrup 1984; Fitzpatric 1986). Hamilton (1964) concurred in the view that altruism is most likely to evolve in "viscous" populations, with little mobility between local groups. Thus, the relevance of group selection has been clearest for species with low vagility.

The reason for the peculiar behavior of the present model (and of the model in Harpending and Rogers 1987) is that, under selective emigration, mobility has two opposing effects. Low mobility increases variance among groups in the frequency of altruists, thereby increasing variance in emigration rates. However, low mobility also means that few emigrants will be accepted into groups. The second of these factors reduces the effectiveness of selective emigration but not that of selective extinction. Wright (1977) distinguished among three phases in his "shifting-balance" theory of evolution: (1) random drift, (2) mass selection, and (3) interdeme selection. He was aware (pers. comm.) that only the first phase is facilitated by isolation, whereas the third is facilitated by mobility. If one thinks of these phases as occurring sequentially, with several generations of drift followed by a change in conditions that leads to several generations of mass and interdeme selection, then the issues considered here do not arise. But if the phases are concurrent, then the conflicting requirements of phases one and three are pitted against each other. The result, at least in the present model, is that selective emigration is facilitated by high levels of migration. This seems to contradict Wright's belief (quoted above) that intermediate levels of migration are most favorable to the process.

Selective emigration is also facilitated by isolation by distance, but only weakly. Since Wright's (1943) early work on the subject, it has often been noted that isolation by distance generates much more genetic differentiation in habitats of one dimension rather than two (Kimura and Weiss 1964; Crow and Aoki 1984). It is usually assumed that this implies a much greater scope for mechanisms of group selection. However, these findings refer to equilibria that are approached so slowly that they apparently have little effect on the opportunity for selective emigration. Finally, selective emigration is facilitated by kin-structured migration, but this effect also seems comparatively weak.

The only factor with any major effect is local group size. This is not necessarily the same as the size of a deme, or breeding group, because the model also applies at the high-migration limit, where the entire population is a single deme. Regardless of the pattern of migration, the local group is the arena within which social interactions are confined. It is what Wilson (1984) called a *trait group*. Selective emigration is most likely to be important when local groups, or trait groups, are small, regardless of the rate or pattern of migration among groups.

Will Selective Emigration Ever Be Important?

The results of this study may be interpreted as implying that selective emigration is of only minor importance compared with kin selection between relatives. Altruism can evolve by selective emigration only if g/c exceeds a number of order $2n$. By comparison, altruism between full sibs can evolve by kin selection if $b/c > 2$ (Hamilton 1964). Thus, selective emigration between groups of size n is at an n-fold disadvantage compared with kin selection within families.

However, it may be unfair to compare the costs and benefits of altruism under kin selection with those under selective emigration. Under kin selection, altruism must be directed preferentially toward kin, whereas under selective emigration, it may be directed indiscriminately within the group. If preference for kin increases the cost of altruism 100-fold, then selective emigration may be as important as kin selection in groups of size 100. Thus, it may not be safe to assume that selective emigration is negligible.

The model studied here is unfavorable to the action of selective emigration in several respects. For example, it ignores the possibility that fluctuating selective pressures may increase group differences (Uyenoyama 1979). Its assumption of additive gene effects is also restrictive and probably unrealistic. Whereas individual selection can use only the additive component of genetic variance, selective emigration uses all the genetic variance and is thus at an advantage when nonadditive variance is extensive. This point has been made by Wade (1978) and is implicit in Wright's (1932) notion of an adaptive landscape. Both theoretical (Crow et al. 1990) and experimental (Wade 1984; Wade and McCauley 1984) studies support the view that this effect may be important. In addition, there is evidence of nonadditive genetic differences between populations in both natural (Burton 1987) and captive (Templeton 1987) populations. Thus, the results presented here undoubtedly underestimate the importance of selective emigration.

The contribution of the present paper is to specify the magnitude of the disadvantage that nonadditive gene effects must overcome if selective emigration is to

dominate individual selection within groups. This disadvantage is n-fold, regardless of the level or pattern of migration among groups. This sounds large, but I doubt that it would have shaken Wright's belief in the importance of selective emigration. In his final paper, he observed that "With a thousand local populations, each exploring the field [of variability] a thousand times as rapidly, the rate of evolutionary advance will be a million times as great" (Wright 1988, p. 120).

SUMMARY

Group selection may operate through selective emigration, as Sewall Wright envisioned, as well as through selective extinction. The discrete-generation model of selective emigration developed here yields the following conclusions.

1. The fitness benefit of altruism, $b^{(\bar{p})}$, depends on the frequency of altruists. Consequently, selective emigration is more likely than kin selection or selective extinction to lead to polymorphic equilibria.
2. In contrast to selective extinction, selective emigration is facilitated (weakly) by high levels of mobility between groups.
3. Like selective extinction, selective emigration is facilitated (weakly) by kin-structured migration and by isolation by distance, particularly where the dimensionality of the migration pattern is low.
4. The only factor with any great effect on the strength of selective emigration is the size of the social group within which altruistic interactions occur.
5. Wright emphasized that selective emigration requires a delicate balance between the migration rate and population size, but this balance appears to be less delicate than Wright thought. For any conceivable migration pattern, migration rate, number of groups, and level of kin structure, an allele for altruism is favored only if its benefit-to-cost ratio exceeds a number of the same order as group size.

ACKNOWLEDGMENTS

I am grateful for suggestions from R. Boyd, J. F. Crow, S. Gaulin, H. Harpending, D. S. Wilson, J. Wood, and reviewers. I am especially grateful for the opportunity to discuss these issues with Sewall Wright. This work was supported in part by National Institutes of Health grant MGN 1 R29 GM29593-01.

APPENDIX

PRICE'S DECOMPOSITION

This section shows how $\Delta\bar{p}$, the change in mean allele frequency following one generation of selection, can be decomposed into within-group and between-group components. This decomposition is equivalent to that developed by Price (1970, 1972) and Wade (1985), but it employs a somewhat different notation. The symbols $\bar{p}$, $\bar{p}'$, E{ }, and $\bar{w}_i$ are defined in the text. The change in $\bar{p}$ is

$$\begin{aligned}\Delta\bar{p} &= \bar{p}' - \bar{p}\\ &= \mathrm{E}\{\bar{w}_i(p_i + p_i' - p_i)\} - \bar{p}\\ &= (\mathrm{E}\{\bar{w}_i p_i\} - \bar{p}) + \mathrm{E}\{\bar{w}_i(p_i' - p_i)\}.\end{aligned}$$

The second term in the last line is a weighted average of allele-frequency changes within groups resulting from individual selection and genetic drift. If the number of groups is large, the effect of drift can be ignored. Inserting the standard formula for the change caused by selection (Crow and Kimura 1970, p. 180) produces

$$\begin{aligned}\Delta\bar{p} &= (\mathrm{E}\{\bar{w}_i p_i\} - \bar{p}) + \mathrm{E}\{\bar{w}_i p_i (w_i^{(A)} - 1)\} \\ &= \Delta\bar{p}_{\mathrm{G}} + \Delta\bar{p}_{\mathrm{I}},\end{aligned}$$

where the terms in the second line equal the corresponding terms in the line above, and $w_i^{(A)}$ is the genic fitness of A within group i, relative to the mean group fitness, $\bar{w}_i$. $\Delta\bar{p}_{\mathrm{G}}$ is the group component of selection, and $\Delta\bar{p}_{\mathrm{I}}$ the individual component.

THREE CANONICAL MODELS OF MIGRATION

This section shows how the effective migration rate, m_{e}, is derived for several models of migration. In each model, local groups are of equal size, and a proportion m of each group is composed of immigrants. Analysis proceeds from the *migration matrix*, whose ijth entry is the fraction of individuals in group j composed of immigrants from group i. The migration matrices discussed here are all *circulants* (Karlin 1982); that is, each row is a circular permutation of the one above it. The eigenvalues of such matrices can be obtained from standard formulas (May 1973, p. 198; Graybill 1983, p. 239). Throughout, I assume that systematic pressure (mutation, external immigration, and selection) is negligible.

The "island model" assumes that, in a population of K local groups of equal size, the immigrants into each group are drawn at random from the population as a whole. The migration matrix for this model has a single unit eigenvalue and the rest are $\lambda_i = 1 - m$, for $i = 2, 3, \ldots, K$ (Carmelli and Cavalli-Sforza 1976, p. 355). Applying the definition of m_{e} (Rogers and Harpending 1986, eq. 8), we have

$$\frac{1}{2m_{\mathrm{e}}} \equiv \frac{1}{K-1}\sum_{i=2}^{K}\frac{1}{1-\lambda_i^2} = \frac{1}{2m(1-m/2)},$$

and

$$m/m_{\mathrm{e}} = 1/(1 - m/2).$$

The "circular stepping-stone model" assumes that groups are arranged in a circle and that each exchanges migrants only with its two immediate neighbors. The migration matrix was given by Carmelli and Cavalli-Sforza (1976, p. 341). Its eigenvalues are $\lambda_{k+1} = 1 - m[1 - \cos(2\pi k/K)]$, for $k = 0, 1, \ldots, K - 1$ (May 1973, p. 198; Graybill 1983, p. 239). From this formula, m_{e} is calculated as above.

The "toroidal stepping-stone model" is a two-dimensional analogue of the "circular stepping-stone model" and assumes that groups occupy the nodes of a rectangular lattice on the surface of a torus. The standard model assumes that all immigrants into each group are drawn from its four adjacent neighbors on the lattice. Thus, the diagonal entries of the migration matrix are $m_{ii} = 1 - m$; and the other entries are $m_{ij} = m/4$ if the ith and jth groups are adjacent or $m_{ij} = 0$ if they are not. Analysis of this model is easy because its migration matrix is $\mathbf{M} = \tilde{\mathbf{M}} \otimes \tilde{\mathbf{M}}$, where $\otimes$ denotes the Kroenecker product (Maruyama 1977, p. 141), and $\tilde{\mathbf{M}}$ is the circular migration matrix with parameters $\tilde{K} = K^{1/2}$ and $\tilde{m} = 1 - (1 - m)^{1/2}$. The eigenvalues of $\mathbf{M}$ are easily obtained from those of $\tilde{\mathbf{M}}$. Let $\tilde{\lambda}_i$, with $i = 1, 2, \ldots, K^{1/2}$, be the eigenvalues of $\tilde{\mathbf{M}}$. Then, the K eigenvalues of $\mathbf{M}$ are $\lambda_{ij} = \tilde{\lambda}_i\tilde{\lambda}_j$, for $i,j = 1, 2, \ldots, K^{1/2}$ (Graybill 1983, p. 227). To compute m_{e}, first find the eigenvalues of the circular stepping-stone model with $K^{1/2}$ groups and migration rate $1 - (1 - m)^{1/2}$, use the last equation to convert these to eigenvalues of the torus migration matrix, and then proceed as before to find m_{e}. The computer program used to do these computations is available from the author.

LITERATURE CITED

Aoki, K. 1982. A condition for group selection to prevail over counteracting individual selection. Evolution 36:832–842.

Arnold, A. J., and K. Fristrup. 1984. The theory of evolution by natural selection: a hierarchical expansion. Pages 292–319 *in* R. N. Brandon and R. M. Burian, eds. Genes, organisms, and populations: controversies over the units of selection. MIT Press, Cambridge, Mass. [First published 1982. Paleobiology 8:113–129.]

Burton, R. S. 1987. Differentiation and integration of the genome in populations of the marine copepod *Tigriopus californicus*. Evolution 41:504–513.

Carmelli, D., and L. Cavalli-Sforza. 1976. Some models of population structure and evolution. Theor. Popul. Biol. 9:329–359.

Crow, J. F., and K. Aoki. 1982. Group selection for a polygenic behavioral trait: a differential proliferation model. Proc. Natl. Acad. Sci. USA 79:2628–2631.

———. 1984. Group selection for a polygenic behavioral trait: estimating the degree of population subdivision. Proc. Natl. Acad. Sci. USA 81:6073–6077.

Crow, J. F., and M. Kimura. 1970. An introduction to population genetics theory. Harper & Row, New York.

Crow, J. F., W. R. Engels, and C. Denniston. 1990. Phase three of Wright's shifting balance theory. Evolution (in press).

Eshel, I. 1972. On the neighbor effect and the evolution of altruistic traits. Theor. Popul. Biol. 3: 258–277.

Fitzpatric, J. W. 1986. Group selection reiterated. Science (Wash., D.C.) 234:882–883.

Fix, A. 1978. The role of kin-structured migration in genetic microdifferentiation. Ann. Hum. Genet. 41:329–339.

———. 1985. Evolution of altruism in kin-structured and randomly subdivided populations. Evolution 39:928–939.

Gilpin, M. E., and B. L. Taylor. 1988. Comment on Harpending's and Rogers' model of intergroup selection. J. Theor. Biol. 135:131–135.

Graybill, F. A. 1983. Matrices with applications in statistics. Wadsworth, Belmont, Calif.

Hamilton, W. D. 1964. The genetical evolution of social behaviour, I. J. Theor. Biol. 7:1–16.

———. 1975. Innate social aptitudes in man: an approach from evolutionary genetics. Pages 133–157 *in* R. Fox, ed. Biosocial anthropology. Wiley, New York.

Harpending, H. C., and A. R. Rogers. 1987. On Wright's mechanism for intergroup selection. J. Theor. Biol. 127:51–61.

Karlin, S. 1982. Classifications of selection-migration structures and conditions for a protected polymorphism. Pages 61–204 *in* M. K. Hecht, B. Wallace, and G. T. Prance, eds. Evolutionary biology. Plenum, New York.

Kimura, M. 1983. Diffusion model of intergroup selection, with special reference to evolution of an altruistic character. Proc. Natl. Acad. Sci. USA 80:6317–6321.

Kimura, M., and G. H. Weiss. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49:561–576.

Levitt, P. R. 1975. General kin selection models for genetic evolution of sib altruism in diploid and haplodiploid species. Proc. Natl. Acad. Sci. USA 72:4531–4535.

Lewis, T. G., and W. H. Payne. 1973. Generalized feedback shift register pseudo-random number algorithms. J. Assoc. Comput. Machin. 20:456–458.

Lewontin, R. C. 1970. The units of selection. Annu. Rev. Ecol. Syst. 1:1–18.

Long, J. C. 1986. The allelic correlation structure of Gainj- and Kalam-speaking people. I. The estimation and interpretation of Wright's *F*-statistics. Genetics 112:629–647.

Maruyama, T. 1977. Stochastic problems in population genetics. Springer-Verlag, New York.

May, R. M. 1973. Stability and complexity in model ecosystems. 2d ed. Princeton University Press, Princeton, N.J.

Maynard Smith, J. 1964. Kin selection and group selection. Nature (Lond.) 201:1145–1147.

———. 1976. Group selection. Q. Rev. Biol. 51:277–283.

———. 1982. The evolution of behavior—a classification of models. Pages 29–44 *in* King's College

Sociobiology Group, eds. Current problems in sociobiology. Cambridge University Press, Cambridge.
Nunney, L. 1985. Group selection, altruism, and structured deme models. Am. Nat. 126:212–230.
Pollock, G. B. 1983. Population viscosity and kin selection. Am. Nat. 122:817–829.
Price, G. R. 1970. Selection and covariance. Nature (Lond.) 227:520–521.
———. 1972. Extension of covariance selection mathematics. Ann. Hum. Genet. 35:485–490.
Queller, D. C. 1985. Kinship, reciprocity and synergism in the evolution of social behaviour. Nature (Lond.) 318:366–367.
Rogers, A. R. 1987. A model of kin-structured migration. Evolution 41:417–426.
———. 1988*a*. Three components of genetic drift in subdivided populations. Am. J. Phys. Anthropol. 77:435–449.
———. 1988*b*. Statistical analysis of the migration component of genetic drift. Am. J. Phys. Anthropol. 77:451–457.
Rogers, A. R., and H. C. Harpending. 1986. Migration and genetic drift in human populations. Evolution 40:1312–1327.
Rychkov, Y. G., and V. A. Sheremet'eva. 1980. The genetics of circumpolar populations of Eurasia related to the problem of human adaptation. Pages 37–80 *in* F. A. Milan, ed. The human biology of circumpolar populations. Cambridge University Press, New York.
Slatkin, M. 1981. Fixation probabilities and fixation times in a subdivided population. Evolution 35:477–488.
Templeton, A. R. 1987. Inferences on natural population structure from genetic studies on captive mammalian populations. Pages 257–272 *in* B. D. Chepko-Sade and Z. T. Halpin, eds. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago.
Uyenoyama, M. 1979. Evolution of altruism under group selection in large and small populations in fluctuating environments. Theor. Popul. Biol. 15:58–85.
Uyenoyama, M., and M. W. Feldman. 1980. Theories of kin and group selection: a population genetics perspective. Theor. Popul. Biol. 17:380–414.
Wade, M. J. 1978. A critical review of the models of group selection. Q. Rev. Biol. 53:101–114.
———. 1982. Group selection: migration and differentiation of small populations. Evolution 36:949–961.
———. 1984. Changes in group-selected traits that occur when group selection is relaxed. Evolution 38:1039–1046.
———. 1985. Soft selection, hard selection, kin selection, and group selection. Am. Nat. 125:61–73.
Wade, M. J., and D. E. McCauley. 1984. Group selection: the interaction of local deme size and migration in the differentiation of small populations. Evolution 38:1047–1058.
Wahlund, S. 1975. Composition of populations and of genotypic correlations from the viewpoint of population genetics. [K. M. Weiss, transl.] Pages 224–263 *in* K. M. Weiss and P. A. Ballanoff, eds. Demographic genetics. Wiley, New York.
Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, N.J.
Wilson, D. S. 1984. Individual selection and the concept of structured demes. Pages 272–291 *in* R. N. Brandon and R. M. Burian, eds. Genes, organisms, populations: controversies over the units of selection. MIT Press, Cambridge, Mass.
Wood, J. W. 1986. Convergence of genetic distances in a migration matrix model. Am. J. Phys. Anthropol. 71:209–220.
Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. Proc. 6th Int. Congr. Genet. 1:356–366.
———. 1943. Isolation by distance. Genetics 28:114–138.
———. 1945. Tempo and mode in evolution: a critical review. Ecology 26:415–419.
———. 1951. The genetical structure of populations. Ann. Eugen. 15:323–354.
———. 1977. Evolution and the genetics of populations. Vol. 3. Experimental results and evolutionary deductions. University of Chicago Press, Chicago.
———. 1988. Surfaces of selective values revisited. Am. Nat. 131:115–123.