

Group selection for a polygenic behavioral trait: A differential proliferation model

(migration/altruism/population genetics)

JAMES F. CROW* AND KENICHI AOKI†

*Laboratory of Genetics, University of Wisconsin, Madison, Wisconsin 53706; and †National Institute of Genetics, Mishima, Shizuoka-ken 411, Japan

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ABSTRACT Conditions for natural selection to increase a polygenic behavioral trait are derived for a model in which the population is divided into a very large number of partially isolated groups of variable and varying size. Specifically, we consider an altruistic trait that is deleterious to the individual but raises the mean fitness of the group. We assume, for each generation, that all groups have the same proportion of males, k , at the time of migration and that each group contributes M_f females and M_m males to a pool of migrants, from which M_f females and M_m males are randomly parceled out to each group. This assumption ensures that, at equilibrium between random drift and a low level of migration and neglecting the small per locus effect of selection, each group has the same expected value of Wright's fixation index, $F_{ST} = F$. At equilibrium, this is approximately $1/(1 + 4M_e)$, where $M_e = 2kM_f + 2(1 - k)M_m$. The trait will increase when $(b - c)/c > (1 - F)/2F = 2M_e$, where b is the expected benefit to the group and c is the expected cost of a unit change in the mean value of the altruistic trait. In particular, the group selection analogue of Hamilton's inequality, $c/b < r$, where r is the coefficient of relationship, is obtained. The effect of isolation is enhanced if migration is mainly between adjacent groups and if group splitting is along family lines, as data on population structure of primates seem to indicate.

Although it is widely believed that most behavioral traits are multifactorial, most models for the evolution of altruism have been monogenic. A notable exception is the kin-selection model of Yokoyama and Felsenstein (1). Slatkin and Wade (2) have presented an analysis of group selection on a quantitative character subject to within-group normalizing selection. Their interest, however, was not in altruism and the assumed mechanism of group selection was the differential extinction of groups. (For general reviews and references, see refs. 3 and 4.) Here we consider a polygenic trait in a structured population and inquire into the condition whereby between-group selection can prevail over within-group selection. The form of between-group selection we have in mind is the differential proliferation of subpopulations (i.e., groups). An approach similar to ours has been used by Price (5, 6), Hamilton (7), and Wade (8) to divide the effects of selection into within- and between-group components. While the trait we specifically consider is altruism, the formulation has more general applicability.

We assume that the trait is determined by a number of unlinked or loosely linked genes, acting additively within and between loci, and by an independent environmental component. Later we shall discuss the consequences of relaxing the additivity assumption. The number of loci is assumed to be so large that the effect of selection at any single locus is small and therefore that Hardy-Weinberg ratios can be assumed within each

randomly mating subpopulation and departures from linkage equilibrium will be negligible. We also ignore any possible effect of random drift in producing linkage disequilibrium throughout the population (9, 10). Finally, we assume that selection at individual loci is so small as not to affect Wright's fixation index (11) or the variance of the trait. The within- and between-group variances will, however, be affected by random gene frequency drift and migration.

To fix ideas, consider a quantitative behavioral trait. The trait might, for example, be the magnitude of help (increased fitness) dispensed to others or the probability of giving such help. In any case, the numerical value of the trait increases linearly with the genic value. In addition, the trait is assumed to cause some harm to the individual, this also increasing linearly with the value of the trait.

Conditions for the altruistic trait to increase

Let C be the value of the polygenic trait and A be the fitness of an individual whose trait measurement is C . For the moment, fitness is measured in Malthusian parameters—roughly the logarithm of Wright's fitness measure. The population is divided into subpopulations or groups and P_s is the proportion of all individuals that are in group s .

From the "secondary theorem of natural selection" (12), the rate of change of the mean value of a character correlated with fitness in any subpopulation is the additive genetic covariance of that character and fitness:

$$\dot{C} = \text{Cov}_g(A, C) = B_{AC}V(C). \quad [1]$$

Since we assume Hardy-Weinberg proportions, the average effect and average excess (13) are identical. Thus, $V(C)$ is the additive genetic variance of the trait and B_{AC} is the regression of the average effect of fitness on the average effect of the trait. The Newtonian superior dot indicates the time derivative. This is a special case of equations 20 and 21 of Crow and Nagylaki (14), with complications of dominance, epistasis, and nonconstant fitnesses ignored.

The change in mean value of the character for the entire population caused by selection within the subpopulations is

$$\dot{C} = B_{AC} \sum_s P_s V_s(C) \equiv B_w V_w,$$

where V_w is the average genetic variance of the trait within subpopulations and $B_w = B_{AC}$ is the intragroup regression of fitness on the value of the trait. It is the regression of genic, not phenotypic, values.

We have regarded B_w as a constant. If it is not, we can replace B_w by \hat{B}_w , defined by

$$\sum_s P_s B_s(AC) V_s(C) \equiv \hat{B}_w V_w,$$

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where \hat{B}_w is the average of the B_w values, weighted by the group size and the within-group genic variance of the character. This is an appropriate weighting, since the rate at which selection changes the character is proportional to the genic variance.

By the same methods used in deriving Eq. 1, the rate of change in the mean of the character because of differential growth of the subgroups (between-group selection) is

$$\hat{C} = \text{Cov}(\bar{A}_s, \bar{C}_s) = B'_{AC}V(\bar{C}_s) \equiv B_bV_b.$$

Here, B_b is the genic regression of group mean fitnesses on the group mean value of the trait and V_b is the between-group genic variance of the trait.

Putting these equations together, the rate of change of the mean value of the trait in the whole population is

$$\hat{C} = B_wV_w + B_bV_b. \quad [2]$$

When the trait is fitness itself, this becomes the extended form of Fisher's (13) fundamental theorem of natural selection (ref. 15, p. 241). The relative importance of within- and between-group selection is given by the terms B_wV_w and B_bV_b .

It is more convenient, when considering the effects of migration and random drift, to adopt a discrete-generation model. In this case, Eq. 2 is replaced by

$$\Delta\bar{C} = (B_wV_w + B_bV_b)/\bar{W}, \quad [3]$$

where B_w and B_b are now, and from now on, the within- and between-group genic regressions of Wright's fitness on the value of the trait and \bar{W} is the population mean fitness, again in Wrightian units.

We are especially interested in an altruistic trait for which B_w is negative and B_b is positive. A sufficient condition for the mean value of the trait to increase in the entire population (in addition, of course, to the requisite genic variance) is

$$\frac{B_b}{-B_w} > \frac{V_w}{V_b}. \quad [4]$$

Since V_b is the variance among means, whereas V_w is the variance among individuals, it is expected that V_w will be much larger than V_b . However, restricted migration converts within-group variance to between-group, so the ratio V_w/V_b decreases with the degree of isolation of the subpopulations. If isolation is strong, the condition for increase of the trait is weaker. We now turn to the effects of partial isolation.

Migration between subpopulations

We should like to be able to express the ratio V_w/V_b as a simple function of the degree of isolation of the subpopulations, even when the group sizes are different and changing and taking into account the observed sex differences in dispersal (for review, see ref. 16). To do so, we modify the Wright island model (11) in the following way.

Let the proportion of males be k in all subpopulations at the time of migration. It seems biologically realistic, at least for mammals, to assume that migration occurs after selective mortality but before reproduction. Assume that each subpopulation contributes M_f females and M_m males to a pool of migrants from which M_f females and M_m males are randomly parceled out to each subpopulation. We emphasize that k , M_f , and M_m are assumed to be constant for all subpopulations and for all generations and that M_f and M_m are absolute numbers of migrants.

We assume that the number of subpopulations is so large that there is no decay of overall variability, that no member of the migrant pool returns to its population of origin, and that no two immigrants into a subpopulation come from the same subpopulation. Note that with this model there is no change in the mean

value of the character in the population from migration. The model of a constant *absolute* number of migrants is somewhat contrived but has the desirable property we are after.

After migration, each migrant behaves as a regular member of its new home and mates randomly with others of the subpopulation. The progeny generation is enumerated at young adulthood just before migration starts in the next generation. Changes in subpopulation size due to reproduction or random loss of members do not affect the calculations. The sex ratio at birth is also irrelevant if we assume, as we do, that sex differences in mortality are uncorrelated with the altruistic trait.

Any effects of selection on the fixation index are ignored; this is justified as an approximation by the weak selection on any individual locus contributing to the polygenic trait. The validity of this approximation has been studied numerically by Aoki (17) in a related monogenic model. Our model, as we now show, ensures that at equilibrium between random drift and a low level of migration each subpopulation has the same value of the fixation index F_{ST} .

Consider an arbitrary subpopulation in which there are N_f females and N_m males at the time of migration. The proportion of males, k , is equal to $N_m/(N_m + N_f)$. Let F be the inbreeding coefficient and G be the coefficient of consanguinity. We need not distinguish the sexes in defining F and G , since these quantities are evaluated before migration. Recall that M_f and M_m are the numbers of female and male migrants.

Of the N_fN_m possible matings, $(N_f - M_f)(N_m - M_m)$ are between nonmigrants. Within this group of matings, the probability that two uniting gametes are identical by descent is G . By our assumptions, all other matings are nonconsanguineous. Thus, denoting the inbreeding coefficient in the next generation by F' , we have

$$F' = \frac{(N_f - M_f)(N_m - M_m)}{N_fN_m} G. \quad [5]$$

To obtain the coefficient of consanguinity in the next generation, G' , we note that two homologous genes in two different randomly chosen individuals can be identical by descent only if they are both derived from the nonmigrant fraction or from the same individual in the migrant fraction. If we collect terms, the recursion becomes

$$4G' = \left(\frac{N_f - M_f}{N_f} + \frac{N_m - M_m}{N_m} \right)^2 G + \left(\frac{N_f - M_f}{N_f^2} + \frac{N_m - M_m}{N_m^2} \right) \left(\frac{1 + F}{2} - G \right) + \left(\frac{M_f}{N_f^2} + \frac{M_m}{N_m^2} \right) \cdot \frac{1 + \bar{F}}{2}, \quad [6]$$

where \bar{F} is the population mean of F .

An equilibrium can be obtained by setting $F' = F = \bar{F}$ and $G' = G$ in these equations, where for notational brevity we denote the equilibrium values by F and G . If both M_f/N_f and M_m/N_m are sufficiently small, we have approximately

$$F = G = \frac{1}{1 + 4[2kM_f + 2(1 - k)M_m]}. \quad [7]$$

The convergence to and the accuracy of Eq. 7 were studied by numerical iteration of Eqs. 5 and 6. In these computations, each subpopulation was permitted to fluctuate randomly in size or to grow steadily larger or smaller, and the approximate accuracy of Eq. 7 was verified. Thus, at equilibrium each subpopulation has essentially the same value of the fixation index, F_{ST} , that we are designating by F .

We can define the effective number of migrants, M_e , as

$$M_e = 2kM_f + 2(1 - k)M_m. \quad [8]$$

If $k = 1/2$ or if $M_f = M_m$, M_e reduces to the actual number of migrants, M . In this case, Eq. 7 becomes $F = 1/(1 + 4M)$, the standard formula for equilibrium among groups having constant size and migration rate (11).

When the proportion of males deviates significantly from $1/2$, the effective number of migrants differs substantially, depending on which sex migrates. For example, in chimpanzees, the migrants are mainly adolescent or young females (18). On the other hand, in olive baboons, the migrants are predominantly adult males (19). In both populations, k is roughly $1/3$. Thus, for the same number of migrants, olive baboons have about twice the effective number of migrants as chimpanzees. We should note, however, that the observed migration rates are quite high in both species (18, 19).

Since the expected value of F is the same in all subpopulations and with Hardy-Weinberg proportions and linkage equilibrium, we can write the within- and between-subpopulation genic variances as

$$\begin{aligned} V_w &= V_0(1 - F) \\ V_b &= V_0(2F), \end{aligned} \quad [9]$$

where V_0 is the genic variance in a randomly mating population (11). Substituting Eqs. 7-9 into Eq. 4 gives, as the condition for the trait to increase in the population,

$$\frac{B_b}{-B_w} > \frac{1 - F}{2F} = 2M_e. \quad [10]$$

Relationship to Hamilton's inequality

The quantitative trait is considered to be the frequency and/or the degree of altruistic behavior. Behaving altruistically entails a cost measured in reduced fitness while dispensing a benefit to the subpopulation. The fitness increment to any individual is the sum of the benefits received from all sources.

The trait is determined by additive genes with an independent environmental component. We define c as the expected cost in reduced fitness per unit change in the character, which is $-B_w$. Likewise, $b - c$ is the expected increase in group fitness per unit change in the average value of the character, which is B_b . Therefore, we can replace Eq. 10 by

$$\frac{b - c}{c} > \frac{1 - F}{2F}. \quad [11]$$

The intraclass correlation between genotypic trait values in a subpopulation is

$$r = \frac{V_b}{V_b + V_w},$$

and substituting into this from Eq. 9 gives

$$r = \frac{2F}{1 + F}. \quad [12]$$

Finally, substituting Eq. 12 into Eq. 11 and rearranging yields

$$r > \frac{c}{b} \quad [13]$$

as the condition for the increase of the trait in the population. We have recovered the familiar cost-benefit inequality (ref. 20; for a simple proof in the context of kin selection, see refs. 21 and 22). We have assumed that there is no dominance, but this does not imply that the validity of Eq. 13 in a randomly mating

population requires that the causative genes be without dominance.

From Eqs. 12 and 10, we can express the average coefficient of relationship within a subpopulation, relative to the entire population, as a function of the number of migrants. This is

$$r = \frac{1}{2M_e + 1}, \quad [14]$$

as was shown by Hamilton (7) for a somewhat different model.

Effects of dominance and epistasis

We have assumed that all the genetic variance is additive. If there is dominance and epistasis, this will reduce the first term on the right side of Eqs. 2 and 3 relative to the second. As emphasized in earlier writings (ref. 15, p. 241; ref. 23) within-group selection depends mainly on the additive component of the variance whereas between-group selection depends on the total genetic variance. Thus we should expect that the lower the heritability of the trait, the greater the relative effectiveness of group as opposed to individual selection.

Maintenance of genetic variability

Formally, in this model the mean value of the trait continues to increase indefinitely, because the restricted migration pattern maintains the ratio of between- to within-group variance. Between-group variance is continuously generated by the random sampling of gametes and other factors that contribute to making the effective number smaller than the census number. The group differentiation measured by F attains the quasi-equilibrium value given by Eq. 7 in the balance between random drift and migration. (In the absence of selection, there is a true equilibrium, but with selection, there are small departures; hence the designation, quasi-equilibrium.) By the assumption that the effective number of migrants, M_e , is constant, this structure is maintained regardless of the increase and decrease in the size of groups. The variance of the entire population is maintained ultimately by the process of mutation, and possibly by such factors as heterosis and frequency-dependent selection, along with the variance-conserving power of particulate Mendelian inheritance.

It is expected that large groups will tend to split into new subpopulations. This too will increase the between-group variance if the split is assortative (24). Studies of the Yanomamo Indians (25) show that splitting is such that close relatives stay together. In contemporary macaques (26, 27), group fission appears to proceed along lines of matrilineage.

Although the major mechanism invoked here for the increase of \bar{C} is the differential proliferation of groups, other mechanisms exist. A smaller group usually has a smaller value of \bar{C}_s . Small groups tend to become extinct for nongenetic as well as genetic reasons and this should tend to increase the value of \bar{C} but at the price of reducing the ratio of between- to within-group variance. An equation analogous to our Eq. 10 can be derived from a model of differential group extinction (unpublished data).

Another mechanism that reduces between-group variance is differential migration from large to small groups. In his shifting-balance theory, Wright (ref. 28 and earlier work) envisaged the less successful groups as requiring a mass influx of immigrants to carry them across a saddle. More favorable to the model of this paper is extinction of small groups and assortative splitting of large ones.

Discussion

Many authors, starting with Haldane (24), have considered the possibility that the group structure of early human populations

was important in developing cooperative and altruistic behavior toward members of the group. The point has been especially elaborated by Muller (ref. 29 and earlier work). Yet, the kind of quantitative comparison of theory with data that would be required to reach a decision is only in its infancy. Studies of contemporary group-living primates (18, 19, 30) suggest rather higher migration rates than Eq. 10 would appear to permit. But, on the other hand, we have only very crude ideas of the magnitude of $-B_b/B_w$, and if the migration is more frequent between adjacent than between distant groups, this will permit more migration while still maintaining the same level of group differentiation. If M_e is very small, 1/2 for example, the population comes to have the same relationship between members of a group as sibs in a panmictic population (Eq. 14; see also ref. 7). This would very likely satisfy the conditions for increase of altruism, provided the appropriate genetic variance for such traits exists. Yet such a population would suffer the ravages of inbreeding deterioration, so the outcome is not clear.

The lesser effect of migration between near neighbors in preventing group differentiation can be illustrated by a rather extreme example, the two-dimensional stepping-stone model (31), in which migration occurs only between adjacent groups. In this model, there is a rough correspondence with Eq. 7. M_e in Eq. 7 is replaced by $\pi M_e / (-\ln 2\mu)$, where μ is the mutation rate (32). The stepping-stone model assumes constant size of groups and differs from our model in other ways, such as the introduction of mutation (which has a negligible effect in our model if mutation is much smaller than the migration rate). If $\mu = 10^{-6}$, $(-\ln 2\mu)/\pi = 4.2$; if $\mu = 10^{-5}$, the value is 3.4. Very crudely, one migrant randomly chosen from the whole population, as in the island model, is as effective as three or four when migration is restricted to neighboring groups in determining the equilibrium value of F .

If a species becomes so successful that the population increases greatly and the structure breaks down, then selection for altruism of the type modeled here would cease. As the population becomes increasingly panmictic, the altruists will be selected against. Altruistic traits developed through more immediate kin selection would be more likely to persist.

Whether altruistic genetic traits have developed from the type of population structure modeled here or have been an extension of parental and sib care to less close kin is, we believe, an open question. Our presentation of the model in this paper is not intended as arguing for it in preference to others.

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