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A model of kin selection for an altruistic trait considered as a quantitative character

(altruism/quantitative genetics/evolution/animal behavior)

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ABSTRACT **Conditions for natural selection to favor increase of a quantitative character are derived for a model in which individuals associate in groups of size n. It is assumed that the logarithm of the fitness of an individual is the sum of two parts, one proportional to the individual's own phenotype, and the other to the mean phenotype in its group. The resulting conditions for the trait to increase under natural selection are analogous to the results found previously in single-locus kin selection models.**

Conditions for the evolution of altruism by kin selection have been developed by Hamilton (1–3). His result was simple: for a gene for altruism to be favored, the ratio of the loss in fitness of the altruist to the gain in fitness of the recipient must be less than the coefficient of relationship between these two. Altruism will be favored by selection only when the two are sufficiently closely related. Kin selection has since been examined in greater detail by Levitt (4) and by Matessi and Jayakar (5), whose results are roughly compatible with those of Hamilton.

In all of these studies it has been assumed that a single gene for altruism is segregating. Hamilton (1) suggested that his criterion would also apply to multifactorial inheritance of the trait, but provided no proof. In this note we obtain conditions analogous to Hamilton's for a model in which the propensity towards altruism is a polygenic quantitative character.

We consider a quantitative character x, which measures the propensity toward altruistic behavior. It is assumed to be distributed in an infinite diploid population according to a normal distribution with mean μ and variance σ^2. The assumption of a normal distribution will be valid if the phenotype is the sum of effects at an infinite number of loci, each of infinitesimal importance (plus an environmental effect). Under some circumstances (6) a model with a finite number of loci will show a normal distribution of the phenotype if there are an infinite number of alleles at each locus, and the allele effects are normally distributed.

During the relevant period of their life, the organisms are assumed to associate in groups of size n, such that the joint distributon of phenotypes of the n individuals is assumed to be multivariate normal, with phenotypic correlation coefficient r between all pairs of members of the group. Their joint distribution is then

$$f(x) = \frac{1}{(2\pi)^{n/2}|V|^{1/2}} \exp\left[-\frac{1}{2}(x-\mu)'V^{-1}(x-\mu)\right] \quad [1]$$

in which

$$\mu' = (\mu, \mu, \cdots, \mu)_{1\times n}$$

and

$$V = \sigma^2 \begin{pmatrix} 1 & \cdots & r \\ \vdots & \ddots & \vdots \\ r & \cdots & 1 \end{pmatrix}_{n\times n}$$

After association into groups, the fitness of each individual is determined as a function of its own phenotype and that of the other members of the group. The particular assumption we make is that the fitness of the ith member of the group is a product of two factors, one dependent only on its own phenotype, and the other only on the mean phenotype of all members of the group. In particular:

$$w_i(x) = e^{-\alpha x_i} e^{\beta \bar{x}} = \exp[-\alpha x_i + \beta \Sigma x_j/n]. \quad [2]$$

Note that the phenotype x_i affects $\bar{x}$, so that the ith individual's effect on its own fitness is the factor $\exp[(-\alpha + \beta/n)x_i]$. Expression 2 is assumed to be the same for all $i = 1, 2, \cdots, n$, so that the numbering of individuals within each group is completely arbitrary: the model is symmetric. The exponential function 2 is chosen purely for convenience, because it maintains the multivariate normality of the joint phenotype distribution after selection, thus avoiding the necessity of considering higher moments of the distribution. When α and β are small, it approximates linear dependence of fitness on the x_i.

The fitness $w_i(x)$ is the contribution of the ith individual, in a group whose phenotype vector is x, to the gametes that form the next generation. The groups of individuals are "trait groups" whose members affect one another's fitnesses. Population density regulation is assumed to take place with respect to the whole population, but not separately within each group. Mating may or may not be within the group: this point is briefly discussed below. Wilson (7, 8) and Charnov (9) have presented single-locus models involving the evolution of altruism in trait groups. To obtain the distribution of phenotypes among individuals "after selection," we consider the distribution of individuals weighted by their fitnesses. By the symmetry of the selection scheme, we need only consider the first individual in each group. Weighting each group by the fitness of its first individual, the joint distribution of phenotypes is

$$h(x) = w_1(x) f(x)/E_x[w_1(x)], \quad [3]$$

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the denominator being the average value of the weighting factor $w_1(x)$ over all groups. $w_1(x)$ is of the form $e^{\tau' x}$, in which

$$\tau' = (-\alpha + \beta/n, \beta/n, \cdots, \beta/n), \quad [4]$$

and a straightforward consideration of the moment generating function of the multivariate normal distribution shows that the denominator of Eq. 3 is

$$E(e^{\tau' x}) = e^{\tau'\mu + 1/2\tau' V\tau}. \quad [5]$$

Using Eq. 1 we then find that $h(x)$ is a multivariate normal distribution with mean $\mu + V\tau$ and covariance matrix V. Thus the marginal distribution of x_1 weighted by $w_1(x)$ is normal with mean

$$\mu + \sigma^2[-\alpha + \beta/n + (n-1)r\beta/n] \quad [6]$$

and variance σ^2. Because the same must be true for all n members of the groups, this gives the marginal distribution of phenotypes, weighted by their fitnesses, for the whole population.

Thus the condition that selection favors increase in the phenotype is simply that $\sigma^2 > 0$ and that

$$-\alpha + \beta/n + (n-1)r\beta/n > 0. \quad [7]$$

We are interested here only in the case in which α and β are both positive. If $n = 1$ we have individual selection, so that condition 7 requires that $-\alpha + \beta > 0$, which is simply the requirement that increasing an individual's phenotype increase its own fitness. When $n > 1$ we find that 7 requires that

$$r > \left(\frac{n}{n-1}\right)\left(\frac{\alpha - \beta/n}{\beta}\right). \quad [8]$$

Note that $\alpha - \beta/n$ is the coefficient measuring an individual's phenotype's negative effect on its own log fitness, and β is the coefficient measuring its effect on the fitness of others. Each of the $n-1$ other individuals in the group receives an increment of β/n in its log fitness, so that in a very limited sense the right side of 8 is the ratio of an individual's reduction of its own fitness to its increase of the fitness of its fellows.

When we prefer to assume that an individual receives no benefit from its own altruism, but only from that of others, expression 4 must be replaced by

$$\tau' = [-a, b/(n-1), \cdots, b/(n-1)]. \quad [9]$$

This amounts to the substitution $a = \beta/n$ and $b = (n-1)\beta/n$, yielding the condition

$$r > a/b. \quad [10]$$

Another case easily considered is when the benefit from altruism increases with the size of the group, so that

$$w_1(x) = e^{-\alpha x_1 + \beta \Sigma x_i}, \quad [11]$$

in which case a similar direct substitution leads to the condition

$$r > (\alpha - \beta/n)/(n-1)\beta, \quad [12]$$

which would be a much weaker condition than 8 if the values of β could fairly be assumed to be comparable in the two cases.

So far we have simply examined the condition for natural selection to increase the phenotype x during a single generation, and have not inquired whether this increase is in fact inherited. The correlation r has been the *phenotypic* correlation between group members. If the heritability of the trait were unity, the condition on r for increase in the phenotype would necessarily also be the condition for selection to favor genes that increased the trait. It may fairly be inquired how the conditions are altered if we assume that the trait is only partly heritable.

To examine this, we add a new variable g, the breeding value of individual 1 for the altruistic trait. Adding a new entry to the vector τ, we must still have the fitness depend only on the phenotypes, so that

$$\tau' = (0, -\alpha + \beta/n, \beta/n, \cdots, \beta/n) \quad [13]$$

and we add a new first row and column to the covariance matrix V, so that it becomes

$$V = \sigma^2 \begin{pmatrix} h^2 & h^2 & ch^2 & \cdots & ch^2 \\ h^2 & 1 & r & \cdots & r \\ ch^2 & r & 1 & & r \\ \cdot & & \cdot & & \\ \cdot & & & \cdot & \\ \cdot & & & & \cdot \\ ch^2 & r & r & & 1 \end{pmatrix}, \quad [14]$$

in which h^2 is the conventional heritability. A careful consideration of the new row and column of 14 will disclose that it assumes that there is no genotype–environment covariance with respect to trait x. The factor c is dependent on how much of the covariance between individuals is additive genetic covariance. In particular, c is such that the additive genetic covariance between group members is $ch^2\sigma^2$. If the association between group members is purely phenotypic assortment, without regard to whether their phenotypes are similar due to genetic causes, then $c = r$. If the association is primarily additive, then genetic $c > r$, and if it is primarily due to common environment or dominance effects, then $c < r$.

The marginal distribution of the breeding value after selection can be obtained in exactly the same way as before. The condition for selection to cause increase in the breeding value turns out to be

$$h^2(-\alpha + \beta/n) + ch^2(n-1)\beta/n > 0, \quad [15]$$

which amounts to the requirements that $h^2 > 0$ and that

$$c > \left(\frac{n}{n-1}\right)\left(\frac{\alpha - \beta/n}{\beta}\right), \quad [16]$$

so that the conditions on c are the same as those on r. Thus, whether partial heritability of the trait loosens or restricts the conditions for the evolution of altruism depends on whether the covariance between group members is primarily additive genetic or primarily nonadditive. For groups of kin who also live in a similar environment, but in the absence of genotype–environment covariance, it turns out that c is precisely the coefficient of kinship between the group members, so that 16 is reminiscent of Hamilton's original result.

We have not so far been specific about the mating system in this model. We may assume that after selection in each generation, the groups dissolve so that mating is at random among the whole population. This is a rather special assumption, but it seems likely that other mating schemes will usually not affect the conditions for increase of the trait. Generally, with artificial selection of quantitative characters, the use of assortative or disassortative mating may alter the rate of response to selection but not the direction of response.

In the above development, we examined the breeding value of the trait under the assumption that it was inherited, while the environmental deviation was not. Humans have many forms of inheritance of environment, the most dramatic being cultural inheritance (of which this paper is an example). In the presence

of cultural inheritance these results would be greatly changed. Examination of cultural inheritance in genetic models is still rudimentary, with the primary concern being to see to what extent extremely simple schemes of cultural inheritance can mimic the effects of genetic inheritance (10–14). It will probably not be fruitful to use models like the present one to examine cultural inheritance, which is not dependent for its driving force on the viability or reproduction of individuals. But it is clear that the presence of cultural evolution severely limits the applicability of the present model to humans.

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