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ALLELE-FREQUENCY CHANGE IN A
CLASS-STRUCTURED POPULATION

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In a population in which there are different classes of individuals, it may not be clear how to assess the consequences of behavior that affects the fitness of individuals of more than one class. Sex (two classes: male and female) and age structure (one class for every age) are two common examples of such a class structure. Other examples might include different lifetime reproductive tactics (territorial and sneaker males; Gross and Charnov 1980), different sizes (large and small females), or, more generally, different fitness classes of individuals.

The problem I am concerned with can be nicely stated in inclusive-fitness language (Hamilton 1964, 1970). Suppose I am an "actor" contemplating two alternatives: one to benefit a class-1 recipient, and the other to benefit a class-2 recipient. How do I assess the relative value to me of these alternatives? The standard inclusive-fitness method requires that I weigh each benefit by my relatedness to the potential recipient, but what is not clear in this case is how I calculate the benefit itself. Typically, benefit should be measured as increased numbers of offspring, but suppose the two recipients have a different class distribution among their offspring. To compare benefits, I require some way of comparing offspring belonging to different classes. The general question is how I obtain an overall "currency" for comparing the fitnesses of recipients belonging to different classes when they have different class distributions of offspring.

The answer, as we shall see, is that a correct numerical measure of fitness can be obtained by calculating a weighted average of the numbers of offspring of each class, using class-specific reproductive values as weights.

The importance of this notion of reproductive value has long been recognized in models with two sexes (Price 1970; Oster et al. 1977; Benford 1978; Stubblefield 1980; Pamilo and Crozier 1982; Frank 1986; Grafen 1986; Taylor 1988) and in age-structured models (Fisher 1930; Leslie 1948; Charlesworth 1980*b*), but it arises more generally whenever there is a natural class structure that interacts with individual fitness. My purpose here is to define these reproductive values in a general setting and to show how their role as weights in an inclusive-fitness calculation arises out of Price's (1970) covariance formula for allele-frequency change.

There are a number of examples in which individuals of different classes might have different class distributions of offspring. First, if we are dealing with size classes, the offspring of a large parent may have a different probability of being large than the offspring of a small parent. Second, the dichotomy of territorial and sneaker males mentioned above provides such an example if sons of territorials are more or less likely to be territorial than are sons of sneakers (however, there is no evidence of this in Gross and Charnov 1980).

A third example is that of age structure. A mathematically simple way to work with an age-structured population is with a model of nonoverlapping generations in which, in each period, we have a new population of individuals, every one of which is counted as an "offspring" of some individual of the preceding period. For example, the reproductive output of a year-3 individual counts his year-1 offspring (the number of his natural children that will survive to the following year) and then must include p year-4 offspring, where p is his probability of surviving another year. Thus, in this approach, individuals of different age classes may have different fecundities, but, more important, they differ in terms of the age mix of their offspring, and the general results of this paper apply (and the fitness matrix w defined below is the Leslie matrix [1948]).

A fourth example is provided by a sexual population in which males and females have different sex ratios of offspring. This can happen in two interesting ways. With haplodiploidy, males and females make different genetic contributions to the offspring of each sex, and, since we count offspring according to genetic contribution, males and females essentially have different sex ratios (males have no sons). This also occurs, even with diploidy, when there are two generations in each "period" but males and females have differential survival from the first generation to the second (partial bivoltinism). This sets up a selective pressure for different sex ratios in the two generations (Seger 1983), which, in turn, causes males and females at the beginning of one period to have different genetic representations in the two sexes that begin the following period.

ASSUMPTIONS AND NOTATION

Formally, I assume discrete, nonoverlapping generations, though I hasten to say that one of the important applications of the method is to a discrete-generation age-structured population. In this case, as mentioned above, an individual of age k who survives to the following year with probability p is regarded as contributing p offspring to age class $k + 1$. I assume a class structure in the population, of unspecified type, such that every individual belongs to one class and may have offspring belonging to any class. My model of behavior assumes a single locus with two alleles: a "normal" allele, which codes for a common behavior, and a "mutant" allele, which causes, in a way to be specified by the dependence of phenotype on genotype, a deviation from the common behavior. I do not assume weak selection (thus, the deviation need not be small), but I assume that the mutant allele is rare, and my equations are valid to the first order in the mutant-allele frequency.

I now summarize the notation (a “prime” on a variable denotes its value in the next generation):

n_j is the number of individuals in class j ;

$N (= \sum_j n_j)$ is the total number of individuals;

$r (= N'/N)$ is the growth rate of the population;

$u_j (= n_j/N)$ is the proportion of individuals in class j ;

Q_j is the frequency of the mutant allele in class j ;

w_{ij} is the average i fitness of class j , defined as the average number of class- i offspring per class- j individual, where offspring must be weighted according to genetic contribution (with age classes, this is the Leslie matrix);

$w_i (= \sum_j w_{ij} u_j)$ is the average i fitness over the population;

$p_{ij} (= w_{ij} u_j / w_i)$ is the probability that a random class- i offspring allele comes from class j ;

c_j is the reproductive value of class j , defined as the probability that a random allele in the future gene pool will derive from a class- j allele in the current generation (note that $\sum_j c_j = 1$);

$v_j (= c_j / u_j)$ is the average reproductive value of a class- j individual, defined as the relative (to other classes) contribution of a class- j individual to the future gene pool of the population, normalized so that average reproductive value is one,

$$\sum_j u_j v_j = 1; \quad (1)$$

$Q (= \sum_j c_j Q_j)$ is the measure of average mutant-allele frequency obtained when each individual is weighted by his reproductive value;

x is a random individual;

G_x , the genotypic value of x , is the frequency of the mutant allele in the genotype of x ;

w_{ix} is the i fitness of x , defined as the number of class- i offspring of x , where offspring must be weighted according to genetic contribution; and

$w_x (= \sum_i v_i w_{ix})$ is the measure of the average fitness of x obtained when each offspring is weighted by its reproductive value.

The deviant behavior of the mutant allele can be expected to change many of the above parameters, and in order to keep track of this, I imagine the mutant allele to be equipped with a “switch” that allows it to behave in either the normal or the deviant mode. When the switch is set to “normal,” I say that the mutant allele behaves normally; if the population is large, it can be expected to attain a stable class-frequency distribution in which the u , Q , w , and p parameters have constant values. The above definition of reproductive value makes sense only in such a stable regime, and the above definition therefore assumes that the mutant allele behaves normally. There are other ways of defining reproductive value (see below), but the use of the asymptotic population is intuitively the most natural and follows the spirit of the approaches of Leslie (1948) and Fisher (1930). When the mutant switch is set to “deviant,” all the parameters may change, but since they are all class averages, the change will be small if the population is large and the mutant allele is rare. I assume this to be the case, and my equations hold to the first order in the mutant frequency.

NORMAL BEHAVIOR OF THE MUTANT ALLELE

I now write the dynamic equations for changes in class frequency and allele frequency. First, note that

$$n'_i = \sum_j w_{ij} n_j. \quad (2)$$

Dividing by N , we get

$$ru'_i = \sum_j w_{ij} u_j, \quad (3)$$

which is the equation for class-frequency change. Finally,

$$Q'_i = \sum_j p_{ij} Q_j \quad (4)$$

is the equation for allele-frequency change. This equation assumes that the normal and mutant alleles have the same expected reproductive success; it thus requires that the mutant allele behave normally. In a stable population, the primes can be removed, and the result can be stated in the language of eigenvectors. This eigenvector formulation is not necessary for an understanding of the concepts, but the complementarity between multiplication on the right and on the left is mathematically quite pretty.

The Right-Eigenvector Result

When the mutant behaves normally and the population parameters have stabilized, the class- and allele-frequency vectors are the right eigenvectors for the matrices \mathbf{w} and \mathbf{p} , with eigenvalues r and 1, respectively:

$$ru_i = \sum_j w_{ij} u_j; \quad (5)$$

$$Q_i = \sum_j p_{ij} Q_j. \quad (6)$$

Since the dominant right eigenvector of the matrix \mathbf{p} is constant (the row sums are one), it follows that, at equilibrium, the Q_j 's are constant: when the mutant allele behaves normally, its equilibrium frequency in all classes is the same. By equation (5), the average i fitness, w_i , in the population is ru_i . This is, of course, expected: the average number of offspring of each class must be proportional to class frequency.

In general, if eigenvectors on the right can be interpreted as frequencies, it turns out that eigenvectors on the left have an interpretation as future values. In this case, the asymptotic genetic contribution of a class- j individual is made through her offspring of all classes. Since she has, on the average, w_{ij} class- i offspring, her reproductive value, v_j , must be proportional to the value of her offspring, $\sum_i v_i w_{ij}$. If we multiply both of these quantities by u_j and sum over j , using equations (1) and (5), we see that the constant of proportionality must be $1/r$. I summarize this result as follows.

The Left-Eigenvector Result

When the mutant behaves normally and the population parameters have stabilized, the vector of individual reproductive values (v_j) and the vector of class

reproductive values (c_j) are the left eigenvectors for the matrices \mathbf{w} and \mathbf{p} , with eigenvalues r and 1, respectively:

$$rv_j = \sum_i v_i w_{ij}; \quad (7)$$

$$c_j = \sum_i c_i p_{ij} \quad (8)$$

(Leslie 1948; Charlesworth 1980*b*). Equation (8) follows by multiplying equation (7) by u_j and using the fact that $w_i = ru_i$.

THE COVARIANCE EQUATION FOR CHANGE IN MUTANT-ALLELE FREQUENCY

In the section above, we considered an equilibrium population in which the mutant allele behaves normally. But the behavior of a deviant mutant affects the fitness of certain individuals (in a way that depends on their genotype) and possibly the fitness of others around, and this in turn moves both u_j and Q_j away from their equilibrium values. What we want is a calculation of how all these changes affect mutant-allele frequency.

How are we to measure population-wide mutant-allele frequency? What we need is some weighted average of the Q_j 's, but how are the weights to be chosen? The answer is that each Q_j should be weighted by the class reproductive value, c_j , which is the same as saying that Q is the population-wide average allele frequency with each individual weighted by his reproductive value, v_j . One reason why these are the "correct" weights to use is that, with these weights, Q does not change when the mutant allele behaves normally, no matter how it is distributed among the classes (Uyenoyama, pers. comm.). The best way to see this is to use these weights to calculate Q' from equation (4). If the mutant allele behaves normally,

$$Q' = \sum_i c_i Q'_i = \sum_{ij} c_i p_{ij} Q_j = \sum_j c_j Q_j = Q. \quad (9)$$

The third equality uses equation (8) and, conversely, can hold for all Q_j 's only when equation (8) holds.

I now derive the class-structured analogue of Price's covariance formula, using the following notation: x is a random individual; G_x , his genotypic value (the frequency of the mutant allele in his genotype); and w_{ix} , his i fitness (the number of his class- i offspring). When the mutant allele behaves in a deviant manner, the next-generation allele frequency is

$$Q' = \sum_i c_i Q'_i, \quad (10)$$

where

$$Q'_i = E(G_x w_{ix})/w_i = E(G_x w_{ix})/ru_i + O(Q^2). \quad (11)$$

The second equality follows from the fact that when the mutant behaves normally, average i fitness, w_i , equals ru_i (eq. 5); thus, when the mutant behavior is deviant, the difference between them will be of the first order in the mutant-allele frequency Q . Since $E(G_x)$ is also of the first order in Q , the error in the equation will be of the order Q^2 . (Recall that $O(Q^2)$ denotes a quantity whose quotient with Q^2 remains bounded as Q^2 approaches zero.) Combining equations (10) and (11) and

using the fact that $c_i/u_i = v_i$,

$$Q' = E(G_x w_x)/r + O(Q^2), \quad (12)$$

where

$$w_x = \sum_i v_i w_{ix} \quad (13)$$

is a measure of the average fitness of x , obtained by weighting the component w_{ix} 's by the reproductive value of a class- i offspring. Equation (13) should be taken as the definition of average individual fitness, and equation (12) provides a good reason for using the offspring reproductive values as weights in defining this average.

In order to get a covariance equation for the change in allele frequency, it is necessary to decompose the expectation in equation (12) along the class of x . If E_j and cov_j denote the expectation and covariance over all class- j individuals, x , then, to order Q^2 ,

$$\begin{aligned} Q' &= \sum_j u_j E_j(G_x w_x)/r \\ &= \sum_j u_j [\text{cov}_j(G_x, w_x) + E_j(G_x) E_j(w_x)]/r \\ &= \sum_j u_j [\text{cov}_j(G_x, w_x) + Q_j r v_j]/r, \end{aligned} \quad (14)$$

where we use the fact that $E_j(G_x) = Q_j$ and

$$E_j(w_x) = \sum_i v_i E_j(w_{ix}) = \sum_i v_i w_{ij} = r v_j + O(Q) \quad (15)$$

(from eq. 7). If we perform the summation on the final term in the bracket in equation (14), we get Q . Hence, the change in allele frequency Q over a single generation of selection is

$$\Delta Q = Q' - Q = \sum_j u_j \text{cov}_j(G_x, w_x)/r. \quad (16)$$

This is our class-structured form of Price's equation. It holds only to the second order in the mutant-allele frequency Q .

THE INCLUSIVE-FITNESS FORMULATION

I now translate equation (16) into an inclusive-fitness form. In fact, there are two different forms depending on whether benefit is to be reckoned as an additive or a multiplicative fitness increment.

Additive Benefits

Turn now to a random potential actor y , and let H_y be the probability that he will act. H_y is his phenotypic value, and I assume that it is determined, in some way, by his genotypic value, G_y , and, in particular, that it is positively correlated with G_y . If he does act, I define s_{xy} , the additive benefit to x derived from the mutant behavior of y , to be the resulting additive increment to the fitness of x . I assume that benefits from different actors are additive, such that the fitness of x is

$$w_x = w_x^o + \sum_y s_{xy} H_y, \quad (17)$$

TABLE 1
POSSIBLE RECIPIENTS OF A RANDOM ACT, BY CATEGORY

Category	Class	No. of Individuals	Average Benefit	Relatedness
Aunts	1	n_a	s_a	R_a
Brothers	2	n_b	s_b	R_b
Cousins	2	n_c	s_c	R_c

where the sum is over all actors, and w_x^o is the fitness of x if the mutant allele is normal. This assumption of additivity of benefits from different actors is standard in inclusive-fitness arguments, and it is unlikely to hold unless the benefit attributable to each actor is small.

Recall that w_x measures the number of offspring of x , with offspring of class i weighted by the reproductive value, v_i . It follows that, for equation (17) to hold, the benefits, s_{xy} , must also be so weighted. Thus, the additive benefit to x must measure his extra number of offspring, with class- i offspring weighted by v_i .

After substituting equation (17) into equation (16), the change in mutant-allele frequency, ΔQ , is given by

$$\begin{aligned} r\Delta Q &= \sum_j u_j \text{cov}_j(G_x, w_x^o + \sum_y s_{xy} H_y) \\ &= \sum_j u_j \text{cov}_j(G_x, \sum_y s_{xy} H_y), \end{aligned} \quad (18)$$

since w_x^o is not correlated with G_x .

The behavior of a single actor may affect the fitness of individuals from different classes and may affect individuals from the same class in different ways. To see how these effects are typically organized, it is helpful to have an example. Suppose three categories of individuals may be affected, as tabulated in table 1. For example, on the average, an actor has n_b brothers belonging to class 2 who receive an average benefit of s_b each and whose relatedness to the actor is R_b . Here, the relatedness of the actor y to the recipient x is defined (Michod and Hamilton 1980; Taylor 1988) as

$$R_{y \rightarrow x} = \text{cov}(G_x, H_y) / \text{cov}(G_y, H_y). \quad (19)$$

The inclusive fitness of the actor is defined as the sum of all benefits accruing from his behavior, with each benefit weighted by his relatedness to the recipient (Hamilton 1964, 1970, 1975). In this case, his inclusive fitness is

$$W_I = n_a s_a R_a + n_b s_b R_b + n_c s_c R_c. \quad (20)$$

It is shown in the Appendix that ΔQ and W_I in equations (18) and (20) are equal up to a positive multiplicative constant:

$$r\Delta Q = M \text{cov}(G_y, H_y) W_I / N, \quad (21)$$

where M is the number of actors. It follows from this that W_I has the same sign as ΔQ , and the inclusive fitness is able to tell us whether the mutant allele is increasing or decreasing in frequency. The assumptions needed are those that are

usually required of any inclusive-fitness formulation: that the mutant behavior is rare, and that the (additive) effect of the behavior of several actors on the fitness of a single individual is the sum of the separate effects.

Multiplicative Benefits

Often, the most natural way to compare benefits to different individuals is as multiplicative increments, and in this case the expression for inclusive fitness takes a different form. For example, the actor might wish to compare a 5% increase in the fitness (viability or fecundity) of a class-1 recipient with a 10% increase in the fitness of a class-2 recipient. To translate these to additive benefits, he needs to know the average fitness of class- j individuals, which, from equation (15), is rv_j . His expected additive benefits are then $s_1 = 0.05rv_1$ and $s_2 = 0.10rv_2$ to the class-1 and class-2 recipients, respectively. The resulting multiplicative formulation of the inclusive fitness exhibits the class weights explicitly. Using the example in the table, if I let $f_{a,b,c}$ be the factors by which the fitnesses of aunt, brother, and cousin are increased, then the inclusive fitness of equation (20) becomes

$$W_I = rv_1(n_a f_a R_a) + rv_2(n_b f_b R_b + n_c f_c R_c). \quad (22)$$

In summary, if multiplicative benefits are used, the recipients must be weighted by expected individual reproductive success; in the present model, this is (proportional to) the reproductive value, v_j .

DISCUSSION

Hamilton and Price were the first to realize that the covariance formula for ΔQ provides the mathematical link between inclusive fitness and allele-frequency change (Hamilton 1970; Price 1970). Since that time, a number of papers (Hamilton 1975; Charlesworth 1980a; Seger 1981; Uyenoyama et al. 1981; Michod 1982; Pamilo and Crozier 1982; Uyenoyama 1984; Grafen 1985; Queller 1985; Taylor 1988, 1989) have considered the relationship between these quantities, providing more-general and more-careful formulations. Price's (1970) original paper already understood that in the case of a haplodiploid population, a relative weighting of 2 must be given to the female population for the covariance formula to work, and since that time, this observation has been made repeatedly (Seger 1981; Pamilo and Crozier 1982; Grafen 1986; Taylor 1988). The purpose of this paper is to provide a proper mathematical formulation for the use of such weights in a general class-structured population.

The general principle is that, in a class-structured population, the fitness, w_x , of an individual, x , can be calculated as his total number of offspring, provided that offspring from different classes are weighted by class-specific individual reproductive values, v_i (eq. 13), obtained from the left eigenvector of the fitness matrix (eq. 7). If fitness is calculated in this way, a class-structured form (eq. 16) of Price's covariance formula for allele-frequency change, ΔQ , is valid. With an appropriate modification of the standard argument (Hamilton 1975; Charlesworth 1980a), ΔQ

can be shown to be equivalent to the classical measure of inclusive fitness (eqs. 20, 21).

In fact, the expression (20) for inclusive fitness is identical to the standard formulation, and it is important to notice just where the weights are hidden. When an actor is calculating the average benefit accruing to a category of recipients, he must measure benefit in units of average individual fitness (eq. 13), and for this purpose, the recipient's class- i offspring must be weighted by v_i .

It is important to distinguish between the class reproductive values, c_j , and the individual reproductive values, v_j . I have used v for the latter because this is the notation introduced by Fisher (1930) for the reproductive value of an individual. I have defined v_j as c_j/u_j , but depending on the nature of the classes, it may be either v_j or c_j that is more apt to vary with the class-frequency vector, \mathbf{u} . For example, if the classes are the two sexes, then p_{ij} and c_j are determined by the ploidies and the parental genetic contributions to offspring and are independent of the sex ratio. By contrast, with age classes, if all competition is population-wide and not within cohorts, w_{ij} and v_j are independent of the age distribution. In general, the situation will be intermediate and depend on the intensity of within-class competition.

It is worth emphasizing just when we do and do not have to pay special attention to reproductive value. If individuals from different classes may have different numbers of offspring but do not differ, on the average, in the class distribution of their offspring, then any reasonable measure of average fitness (e.g., total number of offspring) will provide the relative reproductive values, and the usual methods of accounting will be correct. For example, with a male-female structure, this will be the case when the two sexes have the same offspring sex ratio. But if different classes of parents have different class distributions of offspring, then the class-specific individual reproductive values, obtained from the fitness matrix \mathbf{w} (eq. 7), are required in order to compare average fitness between classes.

For example, if high-quality individuals not only have higher fitness than low-quality individuals but also have a different distribution of quality among their offspring, the fitness of individuals of different quality can still be compared by counting offspring, provided that offspring of different quality are weighted by the correct reproductive value.

In some circumstances, the effect of an actor on a certain recipient does not simply increase his number of offspring by an overall amount; it also affects his offspring of different classes differently. An important example of this is found in sex-allocation behavior. If a breeding female alters the sex ratio of her offspring, and there is some local competition for mates or for reproductive resources in the offspring generation, then her behavior will have a different effect on the sons and daughters of a neighboring breeding female; in the calculation of inclusive fitness, these effects must be treated separately. The way to formulate the model in this case is to have the actor belong to the parental generation and the recipients belong to the offspring generation. An example of this calculation, in both a diploid and a haplodiploid population, is given elsewhere (Taylor 1988). In the case of haplodiploidy, not only do the male and female offspring have different class weights, but they also have different relatednesses to the breeding female.

Maynard Smith (1983) suggested that the main service that population geneticists can perform is to specify the circumstances under which inclusive-fitness methods can safely be applied, and this paper is presented in this spirit.

SUMMARY

Suppose that in a population with a class structure, we wish to calculate the change in frequency of an allele under the action of selection. If the allele affects the behavior of individuals in different classes differently and if parents of different classes have different class distributions of offspring, then the allele frequencies in different classes may be different, and any overall calculation of allele-frequency change must decide how to weight the different class frequencies. I show that the correct weights to use are the class reproductive values, and, using these, I formulate a covariance equation for allele-frequency change. This equation also provides the classical inclusive-fitness formulation if benefits (increased numbers of offspring) are calculated by weighting each offspring by the individual reproductive value that pertains to his class.

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APPENDIX

Here I show how the inclusive fitness, equation (20), is related to the allele-frequency change, equation (16). There is an important technical result required, and although it appears in the relevant literature (Hamilton 1975; Wade 1980; Grafen 1985), it deserves to be better known, and I formulate it here. It might be called the group-decomposition theorem for covariances, and it applies when the sample space is decomposed into mutually disjoint subsets called groups. Suppose we have two random variables A and B ; let a_{ki} and b_{ki} be the i th observation of each random variable in group k . Then the covariance of these observations can be decomposed into a within-group and a between-group component:

$$\text{cov}(a_{ki}, b_{ki}) = E[\text{cov}_k(a_{ki}, b_{ki})] + \text{cov}[E_k(a_{ki}), E_k(b_{ki})]. \quad (\text{A1})$$

The first term on the right is the average within-group covariance, and the second term is the covariance of the group averages. The subscript on the E or the cov denotes the group over which the expectation or the covariance is taken.

Now consider the space of all actor-recipient interactions, and group these according to the recipient, x . Thus, in equation (A1), $k = x$, and, for each x , the index i keeps track of all the interactions of x . Then (A1) becomes

$$\begin{aligned} \text{cov}(G_x, s_{xy}H_y) &= E[\text{cov}_x(G_x, s_{xy}H_y)] + \text{cov}[G_x, E_x(s_{xy}H_y)] \\ &= \text{cov}[G_x, E_x(s_{xy}H_y)], \end{aligned} \quad (\text{A2})$$

where the first covariance runs over all x - y interactions. The average within-group covariance is zero because, for each x , G_x does not vary with y . Using equation (A2), equation (18) can be written

$$\begin{aligned} r\Delta Q &= \sum_j u_j \text{cov}_j(G_x, \sum_y s_{xy} H_y) = M \sum_j u_j \text{cov}_j[G_x, E_y(s_{xy} H_y)] \\ &= M \sum_j u_j \text{cov}_j(G_x, s_{xy} H_y), \end{aligned} \quad (\text{A3})$$

where M is the number of actors and the cov_j run over all interactions between an actor and a class- j recipient.

Now, referring to the table, I use the group decomposition again, but this time I group by category of interaction:

$$\begin{aligned} \text{cov}_1(G_x, s_{xy} H_y) &= n_a \text{cov}_a(G_x, s_{xy} H_y) / n_1, \\ \text{cov}_2(G_x, s_{xy} H_y) &= n_b \text{cov}_b(G_x, s_{xy} H_y) / n_2 + n_c \text{cov}_c(G_x, s_{xy} H_y) / n_2. \end{aligned} \quad (\text{A4})$$

For example, in the second equation, the covariance is over all interactions involving class-2 recipients, grouped according to three categories ($k = b, c$, and everyone else); thus, for each k , i runs over all x - y interactions for x in category k . This time, the covariance of the category averages (the final term of eq. A1) is zero since the average of G_x is the same over all categories. Assuming that s_{xy} is independent both of G_x (the actor cannot "know" the genotype of the recipient) and of H_y (the effect of his act is independent of his probability of acting), s_{xy} can be pulled out of the covariance as its category average, and equation (A3) can be written

$$r\Delta Q = M[n_a s_a \text{cov}_a(G_x, H_y) + n_b s_b \text{cov}_b(G_x, H_y) + n_c s_c \text{cov}_c(G_x, H_y)] / N,$$

using the fact that $u_i = n_i / N$. From the definition of the relatedness coefficients in equation (19), we get equation (21).

LITERATURE CITED

- Benford, F. A. 1978. Fisher's theory of the sex ratio applied to social Hymenoptera. *J. Theor. Biol.* 72:701-727.
- Charlesworth, B. 1980a. Models of kin selection. Pages 11-26 in H. Markl, ed. *Evolution of social behaviour: hypotheses and empirical tests*. Verlag Chemie, Weinheim, W. Germany.
- . 1980b. *Evolution in age-structured populations*. Cambridge University Press, Cambridge.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon, Oxford. (Reprinted and revised, 1958. Dover, New York.)
- Frank, S. A. 1986. The genetic value of sons and daughters. *Heredity* 56:351-354.
- Grafen, A. 1985. A geometric view of relatedness. *Oxf. Surv. Evol. Biol.* 2:28-89.
- . 1986. Split sex ratios and the evolutionary origins of eusociality. *J. Theor. Biol.* 122:95-121.
- Gross, M. R., and E. L. Charnov. 1980. Alternative male life histories in bluegill sunfish. *Proc. Natl. Acad. Sci. USA* 77:6937-6940.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. *J. Theor. Biol.* 7:1-16, 17-52.
- . 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature (Lond.)* 228:1218-1220.
- . 1975. Innate social aptitudes of man: an approach from evolutionary biology. Pages 133-155 in R. Fox, ed. *Biosocial anthropology*. Wiley, New York.
- Leslie, P. H. 1948. Some further remarks on the use of matrices in population mathematics. *Biometrika* 35:213-245.
- Maynard Smith, J. 1983. Models of evolution. *Proc. R. Soc. Lond. B, Biol. Sci.* 219:315-325.
- Michod, R. E. 1982. The theory of kin selection. *Annu. Rev. Ecol. Syst.* 13:23-55.
- Michod, R. E., and W. D. Hamilton. 1980. Coefficients of relatedness in sociobiology. *Nature (Lond.)* 288:694-697.
- Oster, G., I. Eshel, and D. Cohen. 1977. Evolution of social insects. *Theor. Popul. Biol.* 12:49-85.
- Pamilo, P., and R. H. Crozier. 1982. Measuring genetic relatedness in natural populations: methodology. *Theor. Popul. Biol.* 21:171-193.

- Price, G. R. 1970. Selection and covariance. *Nature (Lond.)* 227:520–521.
- Queller, D. C. 1985. Kinship, reciprocity and synergism in the evolution of social behaviour: a synthetic model. *Nature (Lond.)* 318:366–367.
- Seger, J. 1981. Kinship and covariance. *J. Theor. Biol.* 91:191–213.
- . 1983. Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature (Lond.)* 301:59–62.
- Stubblefield, J. W. 1980. Theoretical elements of sex ratio evolution. Ph.D. diss. Harvard University, Cambridge, Mass.
- Taylor, P. D. 1988. Inclusive fitness models with two sexes. *Theor. Popul. Biol.* 34:145–168.
- . 1989. Evolutionary stability in one-parameter models under weak selection. *Theor. Popul. Biol.* 36:125–143.
- Uyenoyama, M. K. 1984. Inbreeding and the evolution of altruism under kin selection: effects on relatedness and group structure. *Evolution* 38:778–795.
- Uyenoyama, M. K., M. W. Feldman, and L. D. Mueller. 1981. Population genetic theory of kin selection, I. Multiple alleles at one locus. *Proc. Natl. Acad. Sci. USA* 78:5036–5040.
- Wade, M. J. 1980. Kin selection: its components. *Science (Wash., D.C.)* 210:665–667.