

Inclusive Fitness Models with Two Sexes

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Received May 4, 1987

Much recent work has focused on the transition from G. R. Price's (1970, *Nature* 227, 520-521) formula for allele frequency change to an inclusive fitness condition for the selective advantage of a certain behaviour. In case there is any kind of asymmetry between the sexes, the analysis must keep track of the two sexes separately, and this leads to a number of different forms of the expression for inclusive fitness. In this paper I gather these forms together and note the assumptions needed to make each valid. I also show how inclusive fitness should be formulated when the behaviour of the actor is controlled by another individual. I illustrate the inclusive fitness approach with a sex allocation example in a haplodiploid population with a local breeding structure. © 1988 Academic Press, Inc.

1. INTRODUCTION

Even with one-locus models of behaviour, the calculation of allele frequency changes can be quite complicated, especially if fitness depends upon the genotype, not only of the individual, but of his neighbours. Other complicating factors include unusual genetic systems or modes of parenting, different behaviour of the sexes, and strong selection.

An elegant expression for allele frequency change is found in Price's (1970) covariance formula. Since that work, a number of papers (Hamilton, 1970; Price, 1972; Charlesworth, 1980; Seger, 1981; Uyenoyama, 1984; Grafen, 1985, 1986; Queller, 1985; Wade, 1985; Frank, 1986a, b, c; and Taylor, 1988) have used this formula to study the selective advantage of a certain behaviour, often in the form of an inclusive fitness condition (Hamilton, 1964, 1972). My purpose is to synthesize and extend this work and to pay particular attention to the formulation in the case that individuals of different sexes have different roles, either behaviourally, or genetically. I also introduce a small extension of the notion of relatedness to include the identity of the individual controlling the behaviour of the actor.

I will suppose we have an infinite population with a periodic life history; I shall refer to one period (which may or may not be a generation) as a

cycle, and I assume cycles are non-overlapping. At a certain point in the cycle, individuals of one or both sexes engage in a particular behaviour, and the objective of the model is to find the equilibrium level of this behaviour. As examples, I have in mind levels of altruistic behaviour, dispersal rates, and sex allocation. To illustrate my results I shall provide an inclusive fitness argument of a sex allocation model of Bulmer (1986) for a geographically structured population.

The mathematical formulation will be somewhat different in the case of *behaviour before mating* (behaviour of offspring) and *behaviour after mating* (behaviour of mated females). Also the second case will have two subcases: in which the behaviour affects the fitness through offspring of different sexes equally or differently. Sex allocation questions are an important example of the second subcase, but there are also others: for example, if a mother alters the dispersal probability of her daughters, this may effect the fitness of her offspring of both sexes, but differently.

In Section 2 I discuss Price's formula; in Section 3 I look at the important notion of the reproductive value of each sex; and in Section 4 I postulate a certain form of the fitness function, generally valid under weak selection, and show that this leads to a formulation of Price's equation in terms of relatedness coefficients. Price's formula is then seen to be equivalent to the inclusive fitness deviation of a mutant individual. In Section 5 I discuss how relatedness is calculated, and in Section 6 I present the sex allocation example.

2. THE COVARIANCE FORMULA

In this section I derive the basic covariance formula for allele frequency change, first following the original derivation of Price (1970), and then in a way that keeps separate track of offspring of each sex.

Imagine a number of alleles at a single locus, and assign to each allele a "score" (the terminology of Grafen, 1985). The score q of an individual is then the average score of the gametes which created him, and for us, q will be a random variable over the population. That is, different individuals will have different q values, and the sample space of this random variable can be regarded as the set of all individuals. An important special case has just two alleles, a "normal" allele with score 0 and a "mutant" allele with score 1, and an individual's score is then the frequency of the mutant allele in his genotype and is called his *genotypic value*.

In the formation of the next generation, let the average score of an individual's gametic contribution to his offspring be $q + \Delta q$. Under fair meiosis, the expectation of Δq over the whole population will be 0. Let W be the fitness of an individual, also a random variable over the population.

For us, W is a measure of the relative number of offspring contributed to the next cycle, but note that W must count full offspring, so that if a female has three mates, each mate gets credited with a third of her offspring. Finally, let Q denote the average individual score over the population.

Currently, $Q = E(q)$, the expected value of q , and after one cycle, Q becomes $Q' = E((q + \Delta q)W)/E(W)$. The change in Q is

$$\Delta Q = Q' - Q = \frac{E(qW)}{E(W)} + \frac{E(\Delta qW)}{E(W)} - E(q). \tag{2.1}$$

Under fair meiosis, or more precisely, under the assumption that W and Δq are uncorrelated, the middle term is 0, and

$$\Delta Q = \frac{\text{Cov}(W, q)}{E(W)} \tag{2.2}$$

which is Price's (1970) formula for allele frequency change. I point out that even when W and Δq are correlated, (2.2) is still valid with an altered definition of fitness. An example of this is found in Uyenoyama's (1984a) study of the evolution of parthenogenesis. But for my purposes it is best to make the assumption that W and Δq are uncorrelated.

Now I will redo the argument in a way that keeps track of the average score of the two sexes separately. Let Q_j be the average score of sex j individuals ($j = 1$ for female and $j = 2$ for male), and let Q'_{ij} be the average score of the gametes contributed by all sex j parents to sex i offspring. To put the two parental sexes together, we must know what is the relative contribution of each parent to the offspring. Let a_{ij} denote the proportion of genes a sex i offspring gets from his sex j parent. Then the average sex i score in the next cycle is

$$Q'_i = \sum_j a_{ij} Q'_{ij}. \tag{2.3}$$

Now I want to average the Q_i to obtain an overall population average score Q , but I want to know whether this should be a weighted average, and if so, what should be the weights? And the correct answer is that sex-specific weights v_i should be chosen so that, in the absence of selection, the overall measure Q should not change. In this case, $Q'_i = Q_j$ and so

$$Q' = \sum_i v_i Q'_i = \sum_{ii} v_i a_{ij} Q'_{ij} = \sum_j \left(\sum_i v_i a_{ij} \right) Q_j = Q$$

and if the last equality is to hold for all Q_j , we must have

$$v_j = \sum_i v_i a_{ij}, \tag{2.4}$$

which says that the vector \mathbf{v} is the left eigenvector of the matrix $A = (a_{ij})$ for the eigenvalue 1. (Note that the row sums of A are 1 and so A must have dominant eigenvalue 1, with constant right eigenvector. It follows that the dominant left eigenvector is positive, and that is what we take \mathbf{v} to be, normalized so that the entries have sum 1.) We can regard v_i as the relative reproductive value of the sex i subpopulation. If the population is at equilibrium, v_i is the asymptotic probability that a random allele many generations in the future derives in the current generation from a sex i individual.

The general formula for population-wide change in the score can now be written

$$\Delta Q = Q' - Q = \sum_{ij} v_i a_{ij} Q'_{ij} - \sum_j v_j Q_j. \quad (2.5)$$

I now look separately at the cases of selection before and after mating. To keep the notation simple, I assume henceforth that Δq is uncorrelated with fitness, and I will ignore the Δq terms.

Selection before Mating

I now consider the behaviour of the offspring before, or perhaps during, the mating process. I suppose that, while this behaviour may affect the number of future offspring of the individual, it will not affect his fitness through male offspring differently from his fitness through female offspring. The average score of sex j individuals is $Q_j = E_j(q)$, where E_j denotes expectation over all sex j individuals. By the above assumption, the same W will measure fitness of an individual through his future offspring of each sex, and

$$Q'_{ij} = \frac{E_j(qW)}{E_j(W)} \quad (2.6)$$

is independent of i . If this is put into (2.5), and (2.4) is used to get rid of the a_{ij} , we get

$$\Delta Q = \sum_j v_j \frac{\text{Cov}_j(q, W)}{E_j(W)} \quad (2.7)$$

which is an average of covariances over each sex. If, as is often the case, $v_1 = v_2$ (more about this in Section 3), and the fitnesses are normalized so the average fitness over males and females is equal, then (2.7) reduces to the classic equation (2.2).

Selection after Mating

I now consider the behaviour of mated females (or perhaps even, in monogamous situations, mated males), and it is convenient to alter our view so that the sample space of our random variables is not the set of individuals, but the set of mated females, or breeding pairs, or breeding events, whatever is appropriate to the type of behaviour under consideration. I denote by q_j the score of the sex j parent (or average score under multiple mating), and by W_i the fitness of the mated female through sex i offspring. Then $Q_j = E(q_j)$, and

$$Q'_{ij} = \frac{E(q_j W_i)}{E(W_i)}, \tag{2.8}$$

and when this is put into (2.5)

$$\Delta Q = \sum_i v_i \frac{E(\sum_j a_{ij} q_j W_i)}{E(W_i)} - \sum_j v_j E(q_j). \tag{2.9}$$

I now consider two subcases. The first is the case in which the behaviour does not affect offspring of different sexes differently. Then, just as in the derivation of (2.7), $W_i = W$ is independent of i , and so also is Q'_{ij} , and (2.9) becomes

$$\Delta Q = \frac{E(\sum v_j q_j W)}{E(W)} - E\left(\sum v_j q_j\right) = \frac{\text{Cov}(q, W)}{E(W)}, \tag{2.10}$$

where q denotes an average parental score:

$$q = \sum v_j q_j.$$

You can think of q as the expected score of a mythical offspring that is made so a proportion v_j of his genes come from his sex j parent.

The second case is the one in which behaviour affects fitness through offspring of each sex differently. Typical of this case is sex allocation behaviour, but this also includes parental manipulation of offspring of a particular sex. In this case, to get (2.5) to look like a covariance, we have to introduce

$$p_i = \sum_j a_{ij} q_j, \tag{2.11}$$

the expected sex i offspring score. Then (2.9) becomes

$$\Delta Q = \sum_i v_i \frac{E(p_i W_i)}{E(W_i)} - \sum_j \left(\sum_i v_i a_{ij}\right) E(q_j), \tag{2.12}$$

where I have used (2.4) to replace v_j in the last term. Using (2.11), we get,

$$\Delta Q = \sum_i v_i \frac{\text{Cov}(p_i W_i)}{E(W_i)} \quad (2.13)$$

in which the covariance is between fitness and offspring genotype.

Equations (2.7), (2.10), and (2.13) are the standard sexual forms of the covariance equation. In the first, we have a population in which individuals of both sexes are interacting. Even if the behaviour to be studied occurs in only one sex, it may affect the fitness of the other, and the overall ΔQ is a weighted average of the covariance terms belonging to each sex. The next two forms really concern breeding behaviour, and our "individuals" are now mated females or breeding pairs. The simpler form (2.10) applies when the behaviour affects fitness through future offspring of both sexes equally. This assumption is also implicitly understood in (2.7). If this fails, we have to use (2.13), in which ΔQ is an average over the two sexes of the covariance of parental fitness through sex i offspring and offspring score.

A special case of (2.13) is worth mentioning. If the genetics is diploid with standard mode of inheritance, then all a_{ij} and v_i are equal to $\frac{1}{2}$, and $p_i = q$, the mean score of the breeding pair. In this case (2.13) can be written

$$\Delta Q = \text{Cov} \left(q, \frac{\bar{W}_1 + \bar{W}_2}{2} \right), \quad (2.14)$$

where $\bar{W}_i = W_i/E(W_i)$ is normalized fitness through sex i . Thus ΔQ becomes the covariance between average fitness and the average score of the breeding pair. This simple form is the reason diploid sex-allocation arguments are easier to make than haplodiploid.

3. REPRODUCTIVE VALUE

Here I will briefly discuss the sex-specific reproductive value vector \mathbf{v} defined in Section 2 as the dominant left eigenvector of the parent-offspring matrix A . I have mentioned that in an equilibrium population, v_i can be interpreted as the asymptotic probability that a random gene from the distant future derives from an individual of sex i . The way to see this is to notice that this probability must be the left eigenvector of A for the eigenvalue 1. This interpretation of \mathbf{v} goes back to Oster, Eshel, and Cohen (1977), Benford (1978), and Stubblefield (1980).

Under the standard mode of inheritance, the v_i are well known. In a

diploid population, all a_{ij} are $\frac{1}{2}$ and so are the v_i , and the weighted averages in Section 2 become straight averages. In a haplodiploid population,

$$A = \begin{bmatrix} \frac{1}{2} & \frac{1}{2} \\ 1 & 0 \end{bmatrix}$$

and $\mathbf{v} = (2, 1)/3$, as was pointed out by Price (1970), Hamilton (1972), Charlesworth (1980b), and Pamilo and Crozier (1982).

Thus asymmetric genetics can cause \mathbf{v} to be non-trivial, but it is important to note that asymmetric parenting can have the same effect. For example, consider the following cycle of partially overlapping generations. The g_0 generation mates at random to produce g_1 . But g'_0 , which starts the cycle again, is formed by random mating of g_1 together with some of the g_0 males, who may survive to mate a second time. If the father of a random g'_0 offspring is g_0 with probability s and g_1 with probability $1 - s$, then under diploidy, the parent-offspring matrix for the cycle is

$$A = \frac{1}{4} \begin{bmatrix} 2-s & 2+s \\ 2-s & 2+s \end{bmatrix}$$

and $\mathbf{v} = (2-s, 2+s)/4$. If $s=0$ we have the standard diploid result, but otherwise, the g_0 males have gained some reproductive value over the females because of the possibility of contributing directly to g'_0 . Examples of this type have been discussed in sex allocation models by Seger (1983), Stubblefield (1986), and Grafen (1986). A similar situation obtains with partial worker-laying of male eggs in eusocial colonies (Charnov, 1978; Benford, 1978).

The notion of reproductive value is useful more generally when contributions from different types of individuals must be combined. A good example is the case of age structure (Charlesworth, 1980b); indeed it was for this purpose that the term was first used (Fisher, 1930). A good recent discussion of reproductive value in models such as this one is found in Grafen (1986).

4. RELATEDNESS

The fitness W of an individual will, in general, depend on his own behaviour, the behaviour of his neighbours, and the average behaviour of the whole population. This direct or "neighbour-modulated" (Cavalli-Sforza and Feldman, 1978; Maynard Smith 1982) form of fitness is the expression we must begin with, because an inclusive fitness formulation will only be applicable if W has a special additive form. If this special form

obtains, the covariances in Section 2 can be made into relatedness coefficients, and the formulae for ΔQ can be interpreted as inclusive fitness deviations.

The form required is that W should depend additively on the phenotypes of the individual and his neighbours. In fact this is rarely the case, even in simple models. What *is* often true, however, is that if behavioural deviations (or more precisely their consequences on fitness) between different genotypes are small, then W will be approximately linear; more precisely, it will be linear to first order in the behavioural deviations. This will hold if W is a differentiable function of the behavioural deviations.

Suppose the behaviour of an individual is specified by a parameter t , which may measure the probability of performing some act, or the intensity of a certain activity, or the proportion of resources allocated to one activity instead of another. Let a specific value t_0 denote *normal behaviour*, and let the *phenotype* H_x of the individual x measure his deviation from normal, so that the behavioural parameter of x is $t_x = t_0 + H_x \delta$, where δ is the deviation of *fully mutant* individual.

Selection before Mating

To study the effect of the behaviour on fitness, I treat the two cases separately and look first at the case of selection before mating, in which both sexes may be present. I will call the individual who expresses the behaviour the *actor* x , and an individual whose fitness is affected a *recipient* y . Even if members of both sexes exhibit the behaviour, we will, at least at the beginning, want to look at behavioural deviations in each sex separately, and, to be specific, I will consider the case of a female actor. Deviations in female behaviour may affect the fitness of both sexes (perhaps differently), and I will also focus on one sex at a time and suppose the recipient is male.

In general the fitness W_y of y could depend on all H_x values in the population. In practice, it will depend on a (small) finite number of H_x and perhaps on the population-wide average \bar{H}_x , and I assume that this is the case. If we normalize so that $W_y = 1$ when $\delta = 0$, and expand W_y in a Taylor series about $\delta = 0$, we get

$$W_y = 1 + \delta \sum_x s_{xy} H_x + \delta c \bar{H}_x + o(\delta), \quad (4.1)$$

where s_{xy} is the *fitness effect of x on y* and is the differential effect of x 's behaviour on y 's fitness per unit increase in t .

If we let G_y denote the genotypic value of y , then the male covariance term in (2.7) can be written, to first order in δ ,

$$\text{Cov}(G_y, W_y) = \text{Cov}\left(G_y, \sum_x s_{xy} H_x\right) \delta. \quad (4.2)$$

It is useful to classify the interactions between x and y by phenotypic effect, and use an index k to keep track of the different possible values of s . Then, breaking the sum up into pieces with the same $s = s_k$, (4.2) becomes

$$\sum_k n_{2k} s_k \text{Cov}_k(G_y, H_x) \delta, \tag{4.3}$$

where n_{2k} is the number of s_k interactions per male, and the covariance is conditional on k .

Now if we shift our scheme of accounting and group interactions by actor x rather than by recipient y , then (4.3) becomes

$$\frac{T_1}{T_2} \sum_k n_{ik} s_k \text{Cov}_k(G_y, H_x) \delta, \tag{4.4}$$

where n_{1k} is the number of s_k interactions per female, and T_i is the proportion of sex i . This is often written as

$$\frac{T_i}{T_2} \sum_y s_{xy} \text{Cov}(G_y, H_x) \delta, \tag{4.5}$$

where the sum is over all y who interact with a fixed x , and the covariance is over the set of interactions with a constant s_{xy} value. When (4.2) is put into the expression (2.7) for ΔQ , it must be divided by average male fitness $E(W_y)$. Since $E(W_y) = 1 + O(\delta)$, from (4.1), and (4.2) is already of order δ , we will get (2.7) to first order in δ , by setting $E(W_y) = 1$.

So far we have considered the effect of the behaviour on male fitness. We also expect an effect on the female population, and the same analysis applies.

If we let z denote a typical female recipient, and make the same assumptions on W_z , we get a similar expression for $\text{Cov}(G_z, W_z)$. As above, we set $E(W_z) = 1$, and plug these into (2.7) to get, to first order in δ ,

$$\frac{v_1 \Delta Q / \delta}{\text{Cov}(G_x, H_x)} = \sum_z s_{xz} R_{x \rightarrow z} + \frac{v_2 / T_2}{v_1 T_1} \sum_y s_{xy} R_{x \rightarrow y}, \tag{4.6}$$

where

$$\begin{aligned} R_{x \rightarrow z} &= \frac{\text{Cov}(G_z, H_x)}{\text{Cov}(G_x, H_x)} \\ R_{x \rightarrow y} &= \frac{\text{Cov}(G_y, H_x)}{\text{Cov}(G_x, H_x)} \end{aligned} \tag{4.7}$$

are the coefficients of relatedness, to an actor x , of a random male and female recipient, respectively, with a given phenotypic effect. The coefficient of the second term on the right can be interpreted as the ratio of the reproductive value of a single male to that of a female. Hamilton (1972) combines this with the relatedness coefficient R to produce what he called a complete or "life-for-life" coefficient of relatedness, but when the genetics or the life history are at all complicated, it is better to keep these components separate.

The right-hand side of (4.6) is called the *inclusive fitness of the behavioural deviation*. It is calculated by taking a random actor and adding up the effects of her behaviour on the fitness of all recipients, each effect weighted by the relative reproductive value of the recipient and by his relatedness to the actor. If the mutant allele tends to cause a positive phenotypic value, then we expect $\text{Cov}(G_x, H_x) > 0$, and the inclusive fitness will have the same sign as $\Delta Q/\delta$, and will thus tell us whether selection favours positive or negative δ ; if inclusive fitness is positive, selection will act to increase t and if negative, selection will act to decrease t . The relatedness coefficients (4.7) are in standard use and were shown by Michod and Hamilton (1980) to be equivalent to a number of other forms. The step from (4.3) to (4.4) constitutes the transition from direct or neighbour-modulated fitness to inclusive fitness (Maynard Smith, 1983).

Selection after Mating

If interactions occur after mating, the situation is the same as if all individuals were the same sex, except that actor and recipient are mated females and genotypic value $G_y = \sum v_i q_i$ is a weighted average of the scores of a female and her mate.

Case 1. Sex allocation unaffected by selection. In this case we can follow the above analysis with a single sex and the inclusive fitness has the form

$$\frac{\Delta Q/\delta}{\text{Cov}(G_x, H_x)} = \sum_y s_{xy} R_{x \rightarrow y}, \quad (4.8)$$

where

$$R_{x \rightarrow y} = \frac{\text{Cov}(G_y, H_x)}{\text{Cov}(G_x, H_x)} \quad (4.9)$$

is relatedness between mated females.

Case 2. Sex allocation affected by selection. In this case the behaviour of x may affect the fitness of y differently through daughters and sons. The analog of (4.1) is the fitness of y through offspring of sex i ,

$$W_{yi} = 1 + \delta \sum_x s_{xyi} H_x + \delta c_i \bar{H}_x + o(\delta), \tag{4.10}$$

where s_{xyi} is the fitness effect of x on y through sex i offspring.

Again we follow the above analysis, but now work from (2.13). Since $E(W_{yi}) = 1 + O(\delta)$, (2.13) can be written, to first order in δ ,

$$\begin{aligned} \Delta Q &= \sum_i v_i \text{Cov}(G_{yi}, W_{yi}) \\ &= \sum_i v_i \text{Cov}\left(G_{yi}, \sum_x s_{xyi} H_x\right) \delta, \end{aligned} \tag{4.11}$$

where G_{yi} is the genotypic value of y 's sex i offspring. As before, the inclusive fitness of the behavioural deviation is

$$\frac{\Delta Q/\delta}{\text{Cov}(G_x, H_x)} = \sum_y \sum_i v_i s_{xyi} R_{x \rightarrow yi} \tag{4.12}$$

where

$$R_{x \rightarrow yi} = \frac{\text{Cov}(G_{yi}, H_x)}{\text{Cov}(G_x, H_x)} \tag{4.13}$$

is the relatedness of y 's sex i offspring to x .

This case, in which the number or quality of offspring of each sex is affected differently by the behaviour, has a more complex inclusive fitness formulation than the previous cases, and involves relatedness of offspring to parent, essentially because, in the calculation of allele frequency change, you have to count separately the effect of the behaviour on the offspring of each sex.

In the case of diploidy with standard inheritance, the formulation is simplified, and we need only use coefficients of relatedness between mated females. In this case, both $v_i = \frac{1}{2}$, and for both i , $\text{Cov}(G_{yi}, H_x) = \text{Cov}(G_y, H_x)$, and (4.12) becomes (4.8) with s_{xy} the average of the s_{xyi} , and $R_{x \rightarrow y}$, the relatedness between mated females, given by (4.9).

5. CALCULATION OF R

In order to calculate R we have to know how phenotype depends on genotype, and the general result is that R is easier to calculate if this dependence is linear. A familiar example is the case in which H_x depends only on

G_x and is 0, h , or 1, depending on whether G_x is 0, $\frac{1}{2}$, or 1. In this case the dependence is linear only if $h = \frac{1}{2}$, the case of additive gene action.

In general H_x may depend on the genotypes of individuals other than x , for example, a neighbour, a sister, or the mother of x , depending on how the behaviour of x is controlled. Seger (1981, Section 5) presents an interesting example, in which x and y are pairs of sisters, and $H_x = 1, \frac{1}{2}$, or 0 depending on whether G_x is greater than, equal to, or less than G_y . This is a case in which H_x depends upon the genotype of two individuals, but in a non-linear way, and it is the non-linearity that makes the calculation difficult.

Usually the behaviour of x is determined by the genotype of a single individual u who "controls" the behaviour of x , and who, of course, might be x himself. In this case H_x will be a function of G_u , and in cases in which it is desired to emphasize the identity of u , I propose that R be written as $R_{x \rightarrow y}^u$ and called "the relatedness of y to x from the point of view of u ." In the special case of additive gene action, in which H_x depends affinely on G_u , R can be written

$$R_{x \rightarrow y}^u = \frac{\text{Cov}(G_y, G_u)}{\text{Cov}(G_x, G_u)}. \quad (5.1)$$

Now (5.1) can be quite difficult to calculate, especially if N is large. What we do in practice is to assume that selection is weak enough (δ small) that the genotypic distribution can be replaced by the neutral distribution ($\delta = 0$). In this case

$$R = R_{x \rightarrow y}^u = \frac{f_{yu}}{f_{xu}} \quad (5.2)$$

(Michod and Hamilton, 1980), where f_{yu} is called the *coefficient of consanguinity between y and u* (Crow and Kimura, 1970, p. 68) and is defined as the probability that random alleles from y and u are identical by descent, and these can be calculated from recursion relations. An example is given in Section 6. Elsewhere (Taylor, 1989) I investigate the extent to which this approximation will give correct equilibrium and stability conditions, and I summarize these results in Section 7.

The form (5.1) is more general than may, at first, appear. If H_x depends on the genotypes of two or more individuals, but in an affine way, a control individual u can be produced as a hypothetical offspring of these individuals, and the above formula applies.

It is also worth pointing out that when the alleles are neutral, the coefficients of consanguinity can be calculated from the "condensed identity

state probabilities" Δ_i (Jacquard, 1974; Michod and Hamilton, 1980) which are independent of allele frequency, and so R is frequency independent. Of course, in practice the alleles will not be neutral, but if selection is weak, R should be "almost" frequency independent and stable polymorphisms should exist only for very narrow ranges of the parameters. Thus, even when H_x depends on the genotypes of individuals other than x , provided this dependence is affine (which in Seger's 1981 example it is not), R should be frequency independent when the alleles are neutral.

6. A SEX ALLOCATION MODEL

As an example of an inclusive fitness argument, I now consider a sex allocation model in an infinite population which breeds on discrete patches, with partial migration among patches. I suppose there are N mated females on each patch, and the offspring mate at random on the patch and then disperse with probability d to a random patch, incurring a penalty c , which I shall regard as a viability cost, and then, on each patch, the native and immigrant mated females compete for the N breeding spots to start the cycle again. The problem is to find the equilibrium sex ratio for these mated females.

The question of dispersal rates in such a population has been studied by Hamilton and May (1977) with a game theoretic model, by Motro (1982, 1983) with a one-locus genetic model, and by Frank (1986c) and Taylor (1988) with inclusive fitness models.

The sex allocation problem was first discussed by Bulmer (1986). The local competition for mates among the males provides a force for female bias (Hamilton, 1967; Taylor and Bulmer, 1980), but the local competition for breeding sites among females (when $d < 1$) creates an opposite force, and it is not at first clear which is stronger. Bulmer (1986) constructed a one-locus genetic model with weak selection and haploid, diploid, and haplodiploid genetics, and various dominance assumptions; and for small values of N he found a moderately female-biased sex ratio, quite insensitive to the dispersal rate. He was prevented from making calculations for large values of N because of the large size of the transition matrix: for $n = 10$, A has 3003 rows and columns. Frank (1986a, b), using an approach similar to mine, has provided an inclusive fitness model for this population under diploidy.

In this section I use the inclusive fitness equation (4.12) for selection after mating, with the assumptions of maternal control of sex allocation, additive gene action, and singly mated females, to find the ESS sex ratio in a diploid and a haplodiploid population. For $N = 2$ and 3, I obtain, as expected, Bulmer's results. Bulmer also considered the companion problem

in which dispersal (with sex-specific probabilities) precedes mating. The calculation of the relatedness coefficients in this case is more complicated (Taylor, 1988), and here I restrict attention to dispersal after mating. There are two parts to the calculation, one to obtain the fitness parameters s_{xyi} of (4.10) and the other to obtain the relatedness coefficients.

Fitness

A deviant mated female will affect her own fitness and the fitness of other females on the same patch, and the effect will differ in the two offspring sexes. So consider a patch with a single deviant female x . Let the normal sex ratio be t_i (proportion of sex i offspring) and suppose x has sex ratio $t_i + \delta_i$. Of course, the t_i sum to 1 and the δ_i sum to zero, but by keeping the two offspring sexes separate, we will more clearly identify the selective forces acting on each. It will be convenient to use the language of gains and losses as if both δ_1 and δ_2 are positive.

I will present the argument in a rather intuitive style; but its correctness can easily be checked with a more rigorous formulation. It will be useful to note that, after the dispersal phase, in which a proportion of d females emigrate but only a proportion of $1 - c$ of these find another patch, the probability that a random female is native to her current patch is

$$k = \frac{1 - d}{1 - d + (1 - c)d} = \frac{1 - d}{1 - cd} \quad (6.1)$$

I measure reproductive success in units of breeding individuals. Since the number of patches is constant, a normal breeding female on a normal patch can expect 1 unit through her offspring of each sex. It is convenient to measure separately the *direct* effect a_i of the extra offspring (on x 's fitness) and the *indirect* effect b_i on the *RS* of all offspring on the patch (including those of x). In the notation of Section 4, $s_{xxi} = a_i + b_i$ and $s_{xyi} = b_i$, if y is a patchmate of x .

I first calculate the a_i . The deviant female x has her normal number of sex i offspring multiplied by $1 + \delta_i/t_i$ and, to zeroth order in δ_i , each of these will have normal reproductive success of 1; so to first order in δ_i , these extra offspring add δ_i/t_i to x 's fitness. Thus

$$a_i = \delta_i/t_i. \quad (6.2)$$

I now count the effect of the extra offspring on the reproductive success of all regular patch offspring. My accounting will always be to first order in the δ_i . There are three categories:

The negative effect α of the extra males on male RS. There are a fixed number of mating spots for males, and the extra males will displace exactly as many regular males, who therefore lose δ_2/t_2 units. Thus $\alpha = \delta_2/t_2$.

The negative effect β of the extra females on female RS. As above, δ_1/t_1 units are lost by regular females somewhere, but note that since the only a proportion k of all reproductive success is won by natives, the extra females will gain only $k\delta_1/t_1$ of these units at home, and here they will displace regular natives with probability k , so the net loss to natives is $\beta = k^2\delta_1/t_1$.

The positive effect γ of the extra females on male RS. The extra females provide δ_1/t_1 units through extra matings for the regular native males. But other native males, mated to native females who are displaced by these extra females, will lose β units, so the net gain is only $\gamma = (1 - k^2)\delta_1/t_1$.

Thus the net gain through females and males is

$$\begin{aligned} b_1 &= -\beta = -k^2\delta_1/t_1 \\ b_2 &= -\alpha + \gamma = -\delta_2/t_2 + (1 - k^2)\delta_1/t_1. \end{aligned} \tag{6.3}$$

If we plug these into (4.12) and set $\Delta Q = 0$ with $\delta_1 = -\delta_2$ we get the equilibrium condition

$$\frac{t_2}{t_1} = \frac{v_2 r_2 - v_2 R_2}{v_1 r_1 - v_1 R_1 k + v_2 R_2 (1 - k^2)}, \tag{6.4}$$

where $r_i = R_{x \rightarrow xi}$ is the relatedness to x of her own sex i offspring, and

$$R_i = \frac{N-1}{N} R_{x \rightarrow yi} + \frac{1}{N} R_{x \rightarrow xi}$$

is the relatedness to x of a random sex i offspring on the same patch (which will be her own with probability $1/N$ and that of a patchmate y with probability $(N-1)/N$). In this form, the equilibrium condition displays the different kinds of effects of the extra offspring: through male *RS* in the numerator and through female *RS* in the denominator. The first term in each records the positive direct effect of the extra offspring, and the second term records the negative indirect effects on relatives of the same sex. The third term in the denominator records the net positive indirect effect of the extra females on related males.

Relatedness

I calculate the relatedness with (5.2), using the coefficients of consanguinity. First note that the coefficients in (6.4) are all relatednesses of a patch offspring to a mated female, with control as the “female part” of the mated female, so they all have the same denominator, the coefficient of consanguinity between a mated female and her female part. Thus we can replace the coefficients by their numerators: the r_i by f_i , the coefficient of consanguinity between a female and her sex i offspring, and the R_i by F_i , the coefficient of consanguinity between a female and a random sex i

offspring on her breeding patch. I now calculate the f_i and F_i from recursion relations.

In the diploid case the calculations are simpler, and I do that first. I let f denote the inbreeding coefficient of the offspring and g the coefficient of consanguinity between two offspring born on the same patch. In an equilibrium population, the values of these coefficients for the next generation can be expressed in terms of the values for this generation by the equations $f' = f$ and

$$g' = \frac{1}{N} \left[\frac{1 + f + 2g}{4} \right] + \frac{N-1}{N} [k^2 g]. \quad (6.5)$$

The two terms on the right correspond to the cases in which the offspring are sibs and not sibs. This equation can be expected to hold only if the number of offspring of each parent is large. These two equations are solved by setting $f' = f$ and $g' = g$, and we get

$$f = g = \frac{1}{4N - 3 - 4(N-1)k^2}. \quad (6.6)$$

The coefficients of consanguinity are

$$f_i = (1 + f + 2g)/4 \quad F_i = g.$$

The second one uses the male-female symmetry under diploidy: the coefficient between a female and a random offspring is the same as that between her mate and the offspring, and so is the same as that between their child and the offspring, again provided the number of offspring is large. If we put these into (6.4) and simplify, we get the equilibrium proportion of males to be

$$t_2 = \frac{N-1}{2N}. \quad (6.7)$$

It is interesting that the sex ratio does not depend on the dispersal probability d . For the case $d=1$ of complete dispersal, (6.7) was obtained by Hamilton (1967, 1979) and by Taylor and Bulmer (1980). For arbitrary d the result was obtained by Bulmer (1986) for the case $N=2$, and for general N by Frank (1986b). Bulmer's results show that, without the assumption of additive gene action, there is a slight dependence of t_2 on d .

I look now at the case of haplodiploidy. The g coefficient defined above must now be replaced by three different coefficients. Let g_{ij} be the coefficient of consanguinity between two individuals of sex i and sex j , born on

the same patch, and let f be the inbreeding coefficient of a female. Then, at equilibrium, $f = g_{12}$ and

$$\begin{aligned}
 g_{11} &= \frac{1}{N} \left[\frac{1+f}{8} + \frac{1}{4} + \frac{g_{12}}{2} \right] + \frac{N-1}{N} k^2 \left[\frac{g_{11} + 2g_{12} + g_{22}}{4} \right] \\
 g_{12} &= \frac{1}{N} \left[\frac{1+f}{4} + \frac{g_{12}}{2} \right] + \frac{N-1}{N} k^2 \left[\frac{g_{11} + g_{12}}{2} \right] \\
 g_{22} &= \frac{1}{N} \left[\frac{1+f}{2} \right] + \frac{N-1}{N} k^2 g_{11}.
 \end{aligned}
 \tag{6.8}$$

These equations solve to give

$$f = g_{12} = \frac{N}{D} \quad g_{22} = \frac{2N-1-k^2(N-1)}{D},$$

where

$$D = k^4(N-1)^2 - k^2(N-1)(5N-1) + N(4N-3).$$

Under haplodiploidy,

$$\begin{aligned}
 f_1 &= (1+f+2g_{12})/4 & F_1 &= g_{12} \\
 f_2 &= (1+f)/2 & F_2 &= g_{22},
 \end{aligned}$$

where we use the fact that a random gene in a mother is the same as the gene in a random son. If we put these into (6.4), with $v_1 = 2v_2$, and simplify, we get the equilibrium proportion of males to be

$$t_2 = \frac{N-1}{2N} \frac{k^4(N-1) - k^2(5N-3) + 4N-2}{k^4(N-1) - k^2(5N-2) + 4N-1}
 \tag{6.9}$$

independent of gene frequency. In Table I some calculated values for $N=3$ and $N=10$ are given. The sex ratio is seen to have a definite female bias,

TABLE I

Equilibrium Sex Ratio t_2 Calculated from (6.9) for Bulmer's (1986) Model of Dispersal after Mating with Haplodiploid Genetics and Dispersal Cost $c=0$

N Patch size	Probability of dispersal d			
	0.01	0.1	0.5	1
2	0.2085	0.2096	0.2130	0.2143
3	0.2964	0.2978	0.3016	0.3030
10	0.4351	0.4358	0.4378	0.4385

stronger for smaller N , and to be rather insensitive to changes in d . The values for $N=3$ are identical to those obtained by Bulmer (1986) for additive gene action.

For the case $d=1$ of complete dispersal, we put $k=0$ and get

$$t_2 = \frac{(N-1)(2N-1)}{N(4N-1)} \quad (6.10)$$

obtained by Hamilton (1979) and Taylor and Bulmer (1980). The case $d=0$ of no dispersal is of interest, because in this case the patches are isolated populations of finite size and the equilibrium sex ratio is $t_2 = \frac{1}{2}$. If we put $d=0$ (which means $k=1$) into (6.9) we get the indeterminate form $\frac{0}{0}$. Taking the limit as k approaches 1, we get

$$t_2 = \frac{(N-1)(3N-1)}{6N^2} \quad (6.11)$$

obtained empirically by Bulmer (1986). It is interesting that the limit of t_2 as d approaches 0 is not the same as, and is in fact less than, the value of t_2 at $d=0$. For example, for $N=4$ (6.11) gives t_2 to be $\frac{11}{32}$. The slightest possibility of sending out an occasional migrant causes the equilibrium sex ratio to jump from $\frac{1}{2}$ down to just about $\frac{1}{3}$.

7. DISCUSSION

The sex allocation problem discussed in Section 6 provides a good example of the power of the inclusive fitness approach in the modelling of behaviour. The calculations required for the exact genetic model for this problem are apparently analytically intractable; the inclusive fitness calculations require care, but are certainly feasible. It is important to notice just what is required for the inclusive fitness approach to work.

The formulae for gene frequency change ΔQ , given in Section 2 in various formulations, are transformed into final formulae for equilibrium behaviour, such as (6.9) in two important steps. The first step provides the inclusive fitness formulations of Section 4, and the second step calculates the relatedness coefficients. In both steps, important simplifying assumptions are made.

First, in order to achieve the inclusive fitness formulations, it is necessary to assume that the fitness of an individual y depends additively on the behavioural deviations of his associates x , and while this may occasionally be strictly true, in most cases of interest, it is true only when selection is weak; more precisely, it is usually true only to first order in the behavioural deviation δ .

Second, we have to calculate the relatedness coefficients, and in models of any complexity, this is considerably easier if the phenotypic value H_x is the genotypic value of some "control" individual, who may be x himself. This is an assumption of additivity of gene action, similar to the assumption (4.1) of additive fitness, but on a different level (within, rather than between, individuals). With this in hand, we then have to be able to calculate covariances between genotypic values, and for this we have to know the full distribution of genotypes, and that can be difficult to get hold of, especially when the population has a local structure with large group sizes. What is required is to find the equilibrium frequency of all the different types (genotypic composition) of groups, and of course this will change as selection acts. In practice, what we do, is to assume $\delta = 0$. In this case, the mutant allele is selectively neutral, the genotypic distribution will reach an equilibrium, and covariances can be calculated from recursive formulae. Of course, we expect this assumption of selective neutrality to be reasonable, only if selection is weak.

Thus, overall, we have an assumption of additive gene action within an individual, and an assumption of weak selection which we use in two different ways, one to get a nice but approximate form of the fitness function and the other to calculate approximations to the covariances. Having made these approximations, will the evolutionary equilibrium state that we calculate (e.g., (6.9)) be correct? Elsewhere (Taylor, 1989) I have shown that the answer is yes. We get the same equilibrium points as if we had used the full fitness function and the exact covariances. Let me emphasize what I mean by an equilibrium point here: If we regard ΔQ as a function of δ , then the equilibrium condition is that it be stationary, that is, that it have zero derivative in δ .

The question of the stability of the equilibrium is more complicated, for there are a number of different types of stability that can be studied. The classic formulation of stability for sex allocation problems, found in Fisher's (1930) original argument, is to suppose the population sex ratio changes by a small amount and to require that mutants which alter their sex ratio in the direction of the equilibrium are more fit. An ESS with this extra stability condition has been called by Eshel (1983) a *continuously stable state*, or CSS, and it is shown in Taylor (1989) that the inclusive fitness calculation, with the above approximations, is capable of correctly identifying this type of stability. I remark that in the example of Section 6, the inclusive fitness function does predict this type of stability. Indeed, the inclusive fitness function gives ΔQ in the form

$$\Delta Q = (\text{DEN}) \delta_1/t_1 + (\text{NUM}) \delta_2/t_2,$$

where NUM and DEN are the numerator and denominator of the right

side of (6.4). The equilibrium condition is $\text{DEN}/t_1 = \text{NUM}/t_2$ and if t_1 is increased above its equilibrium value (and t_2 is decreased) a negative value of δ_1 (and a positive δ_2) will give a positive ΔQ , and a mutant strategy which moves the sex ratio back towards equilibrium will be selected. On the other hand, the standard ESS condition involves looking at the second-order terms in δ , and these are usually lost in the inclusive fitness formulation (Taylor 1989).

The relatedness coefficient R defined in (4.7) originated with Hamilton (1964), and since that time, probably dating from Crozier (1970), has been redefined, generalized, varied, and consolidated (Michod and Hamilton, 1980). One important extension (Uyenoyama, 1984b; Queller, 1985) regards the phenotype H as a genetically determined character and replaces the genetic score G by the additive genotypic value A for the character H (what Falconer, 1960, calls the breeding value). For the simple one-locus two-allele case of this paper, A is affinely related to G , and the definitions are equivalent, but the use of A has a natural extension to multi-allele and multi-locus models (Uyenoyama *et al.*, 1981; Uyenoyama, 1988).

One important thing to note about the coefficient,

$$R_{x \rightarrow y} = \frac{\text{Cov}(G_y, H_x)}{\text{Cov}(G_x, H_x)}$$

is that it is not symmetric in x and y . This was first emphasized by Crozier (1970), and again by Hamilton (1972) and Crozier and Pamilo (1980), who proposed that it should be called the relatedness of y to x , in conformance with the language of regression (if $H_x = G_x$ it is the regression coefficient of G_y on G_x), to emphasize the asymmetry. The way to think of it is as the weighting that x as an actor gives to y as a producer of gametes relative to himself. This formulation emphasizes both the $x - y$ asymmetry and the $G - H$ asymmetry.

To calculate $R_{x \rightarrow y}$ we must specify how H_x is to depend on genotype, and in the usual case H_x will be simply a function of G_x . But if the behaviour of x is controlled by another individual u , then we expect H_x to be a function of G_u , and I have proposed that this be emphasized with the notation $R = R_{x \rightarrow y}^u$. In this case R should be regarded as the weighting that u , as the controller of x 's behaviour, gives to y relative to x as producers of gametes. This formulation is unusual, but it is useful, both conceptually and computationally. An example is found in Taylor (1988) which compares the optimal dispersal rates of offspring from their natal patch under the assumptions of offspring and maternal control of dispersal behaviour. A conventional inclusive fitness approach might be to build two models, one with a mutant offspring, and one with a mutant mother, but a more unified and elegant formulation is to do both cases with a mutant offspring, but to

use different relatednesses between offspring: in one case u is x and in the other, u is the mother of x .

The two formulae for R in Section 5 illustrate the distinction between what are commonly called *relatedness* and *relationship*. Equation (5.1) compares covariances of genotypic values and (5.2) compares probabilities of genetic identity by descent. The first is the relatedness of y to x , and the second is what Pamilo and Crozier (1982) call the *pedigree coefficient of relationship of y to x* . Thus relatedness measures genetic similarity and relationship measures common ancestry (Grafen, manuscript), Crozier (1970), Seger (1981), and Grafen, (1985) discuss the difference between relatedness and relationship, and emphasize that it is relatedness that should be used in inclusive fitness calculations, and this is what can be concluded from Sections 2 and 4. The result discussed in Section 5 is that under certain conditions relationship can be used to measure relatedness. The condition needed for (5.2) to be the same as (5.1) is that two random alleles taken from the two individuals in question must be either identical by descent, or, probabilistically, must look like two alleles taken at random from the whole population. This often holds in models of an infinite population with a simple local structure and selectively neutral alleles, at equilibrium. In finite population models, the result is more problematical, and a discussion of the difficulties is found in Seger (1981) and Grafen (1985).

Finally I look in a general way at inclusive fitness. The inclusive fitness of a behavioural deviation should be thought of as an accounting of the extra number of IBD copies of genes in the "control" u (of the "actor's" behaviour) projected into the future population as a result of the deviation. Typically it is written as a sum over all individuals y whose fitness is affected ("recipients"). Each summand is actually the product of four things, and it is instructive to record the "units" of each of these. I will write a typical summand as

$$(v_i)(1/T_i)(f_{yu})(s_{xy}), \quad (7.1)$$

where y is a recipient of sex i . The reproductive value v_i measures the relative contribution of the sex i subpopulation to the asymptotic gene pool of the population, and so its units are genes per subpopulation. Second, T_i is the number of individuals of sex i (at the time of the interaction) so its units are individuals per subpopulation. Third, f_{yu} is the probability that a random pair of genes from y and u are identical by descent, so it is a measure of the quality of y 's gametes relative to those of u , and so its units are "good" genes per gene where "good" is measured relative to the genes of u . Multiplying the first three terms together, we get units of good genes per individual, through y . Finally, s_{xy} measures extra fitness of y (which is

really extra "individuals") per unit change in the behavioural parameter p , and so the four terms together have units of extra good genes per unit change in behaviour.

In practice, it is usual to normalize (7.1) making things relative to the actor x . Thus, if x is of sex j , v_i and T_i are divided by v_j and T_j , and f_{yu} is divided by f_{xu} to give $R_{x \rightarrow y}^u$ as in (5.2). The expression we finally get is found in (4.6).

ACKNOWLEDGMENTS

An earlier and quite different version of this paper was read and vastly improved by the two referees, Marcy Uyenoyama and David Queller, and also by Alan Grafen, Steve Frank, Bill Stubblefield, and Brian Charlesworth, and I am grateful to them all. Most particularly, they helped me to understand how these ideas relate to previous work. This work was supported by a grant from the Natural Sciences and Engineering Research Council of Canada.

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