

## A GENERAL MODEL FOR KIN SELECTION

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*Abstract.*—Inclusive fitness theory is central to our understanding of the evolution of social behavior. By showing the importance of genetic transmission through nondescendent relatives, it helps to explain the evolution of reproductively altruistic behaviors, such as those observed in the social insects. Inclusive fitness thinking is quantified by Hamilton's rule, but Hamilton's rule has often been criticized for being inexact or insufficiently general. Here I show how adopting a genic perspective yields a very general version that remains pleasingly simple and transparent.

*Key words.*—Altruism, group selection, Hamilton's rule, inclusive fitness, kin selection.

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Hamilton's rule (Hamilton, 1964*a*, 1964*b*) is widely used for understanding the evolution of social interactions. For example, it tells us that an altruistic behavior that costs the performer  $c$  units of fitness and increases its partner's fitness by  $b$  units is favored when  $-c + rb > 0$ , where  $r$  is the relatedness of actors to partners. Despite the direct fitness cost, altruism genes gain because of their presence in relatives. If the product,  $rb$ , is sufficiently large to outweigh the direct fitness cost, then the behavior causes a net gain in *inclusive* fitness. Hamilton's rule has been justified by various population genetic and quantitative genetic models (Hamilton, 1964*a*, 1970; Charnov, 1977; Orlove and Wood, 1978; Charlesworth, 1978; Seger, 1981; Toro et al., 1982; Michod, 1982). But it has often been criticized for being inexact or insufficiently general (e.g., Levitt, 1975; Cavalli-Sforza and Feldman, 1978; Templeton, 1979; Boorman and Levitt, 1980; Karlin and Matessi, 1983; Cheverud, 1984; Lynch, 1987). Various corrections (Michod and Hamilton, 1980; Seger, 1981; Karlin and Matessi, 1983; Grafen, 1985; Queller, 1985) increase the generality somewhat but they also tend to erode the simplicity that has made Hamilton's rule so appealing in the first place. Here I show that when Hamilton's rule fails, it is because costs and benefits are expressed as average effects of phenotypes. If we represent them instead as average effects of genes, a general and simple version of Hamilton's rule emerges.

### THE GENIC MODEL

Consider selection on an altruistic behavior. Let  $G$  represent each individual's genes for the behavior. It could be the individual's frequency of an altruism allele at a single locus, or any linear combination of such frequencies, such as the breeding value of quantitative genetics. Neglecting meiotic drive and genetic drift, the selective change in the population average  $G$ , can be written as

$$\Delta \bar{G} = \text{Cov}(G, W), \quad (1)$$

where  $W$  is relative fitness (Price, 1970).

Now, there exists a least squares multiple regression equation that predicts relative fitness from  $G$  and  $G'$ , the latter representing the average  $G$  value of an individual's neighbors whose performance of the behavior could affect its fitness. Each individual's fitness can therefore be written as

$$W = \alpha + \beta_{WG \cdot G} G + \beta_{WG' \cdot G} G' + \epsilon \quad (2)$$

where  $\beta_{WG \cdot G}$  and  $\beta_{WG' \cdot G}$  are partial regression coefficients and the  $\epsilon$ 's are residuals (the differences between the actual values and the values predicted by the regression). Substitution into (1) gives:

$$\begin{aligned} \Delta \bar{G} = & \text{Cov}(\alpha, G) + \beta_{WG \cdot G} \text{Cov}(G, G) \\ & + \beta_{WG' \cdot G} \text{Cov}(G', G) + \text{Cov}(\epsilon, G). \end{aligned} \quad (3)$$

The first term is zero because  $\alpha$  is a constant and the last term is zero because the residuals are necessarily uncorrelated with the

independent variables. Therefore, genes for the behavior in question increase in frequency ( $\Delta\bar{G} > 0$ ) when

$$\beta_{WG \cdot G'} + \beta_{G'G} \beta_{WG' \cdot G} > 0 \quad (4)$$

where  $\beta_{G'G}$  is the familiar genetic regression definition of relatedness (Hamilton, 1972).

Most approaches to generalizing Hamilton's rule have tried to find more general definitions of relatedness (Hamilton, 1972; Orlove and Wood, 1978; Michod and Hamilton, 1980; Seger, 1981; Grafen, 1985). Several others have attempted to redefine the costs and benefits (Levitt, 1975; Boorman and Levitt, 1980; Karlin and Matessi, 1983), but have failed to find simple and general expressions for them. Formula (4) shows that costs and benefits can be generalized in a simple and intuitively satisfying way, as partial regression coefficients.  $\beta_{WG \cdot G'}$  describes how an individual's fitness changes as a linear function of its own genes if the effects of its neighbor's genes are held constant. Similarly,  $\beta_{WG' \cdot G}$  describes how fitness changes as a linear function of the neighbor's genes when the effects of the individual's own genes are held constant.

#### PHENOTYPIC MODELS

The principal point of this paper is that there is a simple and generally valid version of Hamilton's rule. A secondary point, to be treated in this section, is that other versions and their apparent failures can be understood as special cases of the general result. Most versions of Hamilton's rule express costs and benefits in terms of phenotypic rather than genotypic effects. To recover these forms, and to see why they sometimes fail, the path diagram of Figure 1 can be used.

Instead of mapping directly to fitness, the breeding values are viewed as affecting phenotypic values ( $P$  and  $P'$ ), which in turn affect fitness. The diagram also shows unspecified other factors,  $X$ ,  $X'$ , and  $Y$ , which may also affect phenotypes and fitness. It is these additional factors that can cause failure of the familiar forms of Hamilton's rule. Such additional factors must always be present but they do not cause problems if they are uncorrelated with breeding values ( $G$  or  $G'$ ). In the general genetic formulation (4) derived above, all extraneous factors are

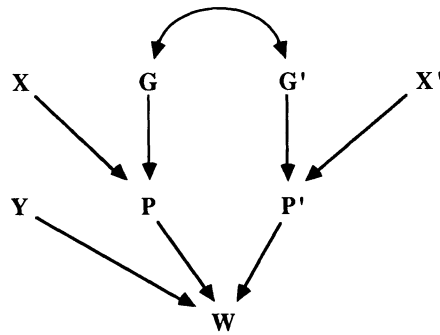


FIG. 1. Path diagram for the effect of breeding values of individuals ( $G$ ) and of their partners ( $G'$ ) on fitness ( $W$ ), by way of phenotypes ( $P$  and  $P'$ ).  $X$  and  $X'$  are any additional factors affecting phenotypes, while  $Y$  represents any additional factors affecting fitness. Here  $X$ ,  $X'$ , and  $Y$  are shown to be uncorrelated with breeding values, but this will not always be true. Although path analysis uses standardized variables, the variables used in this paper are unstandardized.

forced to be uncorrelated with  $G$  by the fact that  $G$  is used as one of the regression predictors of  $W$ .

Now let us use a phenotypic prediction equation:

$$W = \alpha + \beta_{WP \cdot P}P + \beta_{WP' \cdot P}P' + Y. \quad (5)$$

Substituting into Price's Equation (1) gives

$$\begin{aligned} \Delta\bar{G} = & \text{Cov}(\alpha, G) + \beta_{WP \cdot P} \text{Cov}(P, G) \\ & + \beta_{WP' \cdot P} \text{Cov}(P', G) + \text{Cov}(Y, G) \end{aligned} \quad (6)$$

If genes are related to fitness only through phenotypes and not through any other path involving other factors ( $Y$ ), then the last term drops out (along with the first) and  $\Delta\bar{G}$  is positive whenever

$$\beta_{WP \cdot P} + \frac{\text{Cov}(G, P')}{\text{Cov}(G, P)} \beta_{WP' \cdot P} > 0. \quad (7)$$

Here the costs and benefits are represented as partial regressions of phenotypes on fitness. The covariance relatedness ratio form was first suggested by Orlove and Wood (1978). There is a related form,  $\text{Cov}(G', P)/\text{Cov}(G, P)$  (Michod and Hamilton, 1980; Seger, 1981) that is identical provided covariances are taken over all members of the population (Queller, 1985). This phenotypic version of Hamilton's rule is valid subject to the single condition that other factors represented by  $Y$  are uncorrelated with the  $G$ 's.

There will always be variables other than the altruism phenotype affecting fitness, but they will often be uncorrelated with breeding values. An example of the kind of  $Y$  that does cause problems would be another trait affecting fitness that is genetically correlated with the altruism trait. Grafen (1985) has noted that it is not sensible to reject Hamilton's rule for this reason because all evolutionary models are subject to the same criticism. And, as with other models (Lande and Arnold, 1983), the effects of correlated traits can be partitioned out with the use of partial regression coefficients. If we let  $Y$  represent the correlated trait, and assume that any remaining factors are uncorrelated with  $G$ , then substituting  $W = \alpha + \beta_{WP \cdot PY}P + \beta_{WP \cdot PY}P' + \beta_{WY \cdot PP}Y$  into Price's rule (1) yields a modified condition for increase of  $\bar{G}$ .

$$\beta_{WP \cdot PY} + \frac{\text{Cov}(G, P')}{\text{Cov}(G, P)}\beta_{WP \cdot PY} + \frac{\text{Cov}(G, Y)}{\text{Cov}(G, P)}\beta_{WY \cdot PP} > 0. \quad (8)$$

This is Hamilton's rule with an additional term for the effect of the correlated character,  $Y$ . Maternal effects on fitness (Cheverud, 1984; Lynch, 1987) could be treated in a similar manner.

Another kind of problem that can be represented by the  $Y$  pathway sometimes arises from the operation of the social trait itself rather than from correlated characters. Suppose that the social phenotypes of an individual ( $P$ ) and its partner ( $P'$ ) have non-additive effects on fitness, as will be true for many reasonable kinds of social selection (Levitt, 1975; Charlesworth, 1978; Cavalli-Sforza and Feldman, 1978; Templeton, 1979; Macnair and Parker, 1979; Metcalf et al., 1979; Boorman and Levitt, 1980; Karlin and Matessi, 1983). This could be represented by  $Y$  acting as an interaction variable. Such interaction variables will typically be correlated with  $G$ , making (7) invalid. For one simple nonadditive model, Queller (1985, in press) previously derived a version of Hamilton's rule essentially identical to Formula (8), with  $Y$  being the product of  $P$  and  $P'$ . The second covariance ratio was termed a synergism coefficient be-

cause it scales the relative importance of the fitness effect that is due to the synergistic interaction of the two partners.

Though (7) expresses costs and benefits in measurable phenotypic terms, the relatedness coefficient is not easily measured. With some additional assumptions, we can recover Hamilton's (1972) genetic regression coefficient that was used in (4), while retaining the phenotypic cost and benefit forms. To obtain this form, it must be recognized that phenotypes are affected by more than just breeding values. Write them in terms of heritabilities as  $P = h^2G + X$  and  $P' = h^2G' + X'$  and substitute into (7) to obtain

$$\beta_{WP \cdot P'} + \frac{\text{Cov}(G, G') + \text{Cov}(G, X')}{\text{Cov}(G, G) + \text{Cov}(G, X)} \cdot \beta_{WP \cdot P} > 0. \quad (9)$$

The  $X$ 's could represent dominance deviations or environmental deviations, or both. Whenever  $\text{Cov}(G, X) = 0$  and  $\text{Cov}(G, X') = 0$  this reduces to Hamilton's (1972) form:

$$\beta_{WP \cdot P'} + \frac{\text{Cov}(G, G')}{\text{Cov}(G, G)}\beta_{WP \cdot P} > 0. \quad (10)$$

Clearly, this will be true if there is no dominance and no gene-environment correlation. This result can also be obtained under dominance provided there is random mating (Seeger, 1981), because the ratio involving dominance values,  $\text{Cov}(G, X')/\text{Cov}(G, X)$ , is equal to the one involving only breeding values.

## DISCUSSION

The formulation of Hamilton's rule represented by Equation (4) possesses the same high level of generality as Price's Equation (1) because it is derived without any additional assumptions. The gain in generality has been achieved by attributing fitness effects to genes rather than to phenotypes. Using breeding value,  $G$ , in the prediction Equation (2) guarantees that  $\text{Cov}(\epsilon, G) = 0$ , allowing Equation (3) to be simplified. The result is valid even when the relationship between genotype and fitness is complicated by factors such as nonadditive fitness effects, maternal effects, correlated traits, and gene-environment correlation. While For-

mula (4) does not adjust for differences in reproductive value, the methods of Taylor (1990) can be used to do so. Its main limitation is that, like Price's Equation (1), it is not completely recursive (Grafen, 1985).

Despite its generality, this version of Hamilton's rule does not render previous versions obsolete. It may be superior for theoretical uses. But in empirical studies, it is difficult to measure fitness effects of  $G$ ; only phenotypes can be assessed with ease. It will therefore often be necessary to continue using phenotypic costs and benefits, with their added assumptions (see Michod, 1982; Grafen, 1985 for reviews). The real value of this genetic version is that it serves to provide a broader context for inclusive fitness theory.

First, it illuminates the relationship of Hamilton's rule to another method of analyzing social selection, the group selection method. Wade (1985) has derived a very general group selection equation which has been viewed as evidence that the group selection approach is superior (Breden, 1990). In fact, the apparent difference between the two approaches is due to differences in how the two models were formulated. Previous versions of Hamilton's rule have expressed costs and benefits in terms of average effects of behavioral phenotypes. Wade's group selection formula is expressed in terms of fitness effects of genes, and this accounts for its higher level of generality. However, when Hamilton's rule is also expressed in terms of average effects of genes, as in Formula (4), it becomes equally general. It can also be shown that if both models are expressed in terms of phenotypic effects, then they have the same decreased generality (Queller, in press). The two approaches are simply alternative but equivalent ways of analyzing the selection process.

Second, the result derived here provides a context for other versions of Hamilton's rule. Previously, there has been no general version, and Hamilton's rule seemed to be a result that just pops out of mathematical models under certain fortunate conditions. The word "heuristic" has sometimes been used, suggesting that, although inclusive fitness theory sometimes works, it does so in mysterious and perhaps untrustworthy ways. The analysis in this paper shows this view

to be inaccurate. Once cost and benefits are defined in genetic rather than phenotypic terms, Hamilton's rule becomes both general and easy to understand. If we want costs and benefits defined in phenotypic terms then failures sometimes arise due to complications in either the relationship of genes to phenotype or in the relationship of phenotypes to fitness. But it is not difficult to understand the causes of these failures and the additional assumptions required to avoid them.

Finally, the approach adopted here serves to set Hamilton's rule into a wider context of models, and consequently helps to illuminate exactly what inclusive fitness theory does. Note that the multiple regression Equation (2) that is substituted into Equation (1) is very flexible. Specifically, as long as we include the individual's own breeding value,  $G$ , in the equation, we can use any other predictors we choose and still satisfy the condition [ $\text{Cov}(G, \epsilon) = 0$ ] that allows us to arrive at a result like Formula (4). For example, we can subdivide the second predictor into multiple classes. If we let one prime indicate siblings and two primes indicate cousins, then substitution of  $W = \alpha + \beta_{WG \cdot GG'}G + \beta_{WG' \cdot GG'}G' + \beta_{WG'' \cdot GG''}G'' + \epsilon$  into Equation (1) yields a version of Hamilton's rule with separate terms for siblings and cousins ( $\beta_{WG \cdot GG'} + \beta_{G'G} \beta_{WG' \cdot GG'} + \beta_{G''G} \beta_{WG'' \cdot GG''} > 0$ ). We can also include correlated traits in the regression equation to isolate their effects in the final result [as shown for the phenotypic version in Formula (8)]. Environmental effects on fitness can be partitioned out in exactly the same manner. Adjustments of these kinds may be useful when complicating factors intrude in field studies of kin selection.

Thus, inclusive fitness theory turns out to be a fairly special case of a general selection model. Information from relatives is used, perhaps with other predictors, to describe fitness. Presumably, in many particular cases, we could often add more and more predictors to the regression equation and obtain a much better description than could be achieved by simple inclusive fitness theory. But recognizing this enhances rather than diminishes Hamilton's contribution. Hamilton's approach involved two insights. The first was to strip away complicating fac-

tors and focus on the one crucial factor that was both poorly understood and central to the evolution of altruism: reproduction through relatives. Correlated traits and most environmental effects were therefore quite reasonably ignored. The second insight was to forego using all the information potentially available from relatives and to focus instead on a restricted set of relatives, those that actually affect the individual's fitness through their performance of the social behavior in question. This is what elevates inclusive fitness theory from a model using arbitrary predictors to one that is essentially causal in character. Since all fitness effects are attributed to the behaviors that cause them, inclusive fitness theory provides a powerful way for thinking about the evolution of such behaviors.

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