

## Interacting Phenotypes and the Evolutionary Process. II. Selection Resulting from Social Interactions

Jason B. Wolf,<sup>1,\*</sup> Edmund D. Brodie III,<sup>1</sup> and Allen J. Moore<sup>2,†</sup>

1. Department of Biology, Indiana University, Bloomington, Indiana 47405;

2. Department of Entomology, University of Kentucky, Lexington, Kentucky 40546-0091

*Submitted March 5, 1998; Accepted September 23, 1998*

---

**ABSTRACT:** Social interactions often affect the fitness of interactants. Because of this, social selection has been described as a process distinct from other forms of natural selection. Social selection has been predicted to result in different evolutionary dynamics for interacting phenotypes, including rapid or extreme evolution and evolution of altruism. Despite the critical role that social selection plays in theories of social evolution, few studies have measured the force of social selection or the conditions under which this force changes. Here we present a model of social selection acting on interacting phenotypes that can be evaluated independently from the genetics of interacting phenotypes. Our model of social selection is analogous to covariance models of other forms of selection. We observe that an opportunity for social selection exists whenever individual fitness varies as a result of interactions with conspecifics. Social selection occurs, therefore, when variation in fitness due to interactions covaries with traits, resulting in a net force of selection acting on the interacting phenotypes. Thus, there must be a covariance between the phenotypes of the interactants for social selection to exist. This interacting phenotype covariance is important because it measures the degree to which a particular trait covaries with the selective environment provided by conspecifics. A variety of factors, including nonrandom interactions, behavioral modification during interactions, relatedness, and indirect genetic effects may contribute to the covariance of interacting phenotypes, which promotes social selection. The independent force of social selection (measured as a social selection gradient) can be partitioned empirically from the force of natural selection (measured by the natural selection gradient) using partial regression. This measure can be combined with genetic models of interacting phenotypes to provide insights into social evolution.

\* To whom all correspondence should be addressed; e-mail: jwolf@bio.indiana.edu.

† Present address: School of Biological Sciences, 3164 Stopford Building, University of Manchester, Manchester M13 9PT, United Kingdom.

Am. Nat. 1999. Vol. 153, pp. 254–266. © 1999 by The University of Chicago. 0003-0147/99/5303-0002\$03.00. All rights reserved.

*Keywords:* social selection, kin selection, indirect genetic effects, quantitative genetics, Hamilton's rule.

---

Interactions with conspecifics, especially those that result in social competition, can have dramatic effects on an individual's fitness. Individuals compete for access to resources (Stevens et al. 1995; Pusey and Packer 1997), signal for mates (West-Eberhard 1984), provide helping behavior or are altruistic (e.g., Wilkinson 1984), and excrete allelopathic chemicals (Rice 1984)—acts that all have fitness consequences for individuals involved in interactions. Selection resulting from these social interactions, termed social selection (Crook 1972; West-Eberhard 1979, 1983, 1984), differs from ecological selection (i.e., natural selection) because an individual's fitness is not determined entirely by its own phenotype but, rather, is determined in part by the phenotype of its social partners (i.e., the social environment). In fact, social interactions are thought to require or lead to the evolution of traits that can be termed interacting phenotypes (Moore et al. 1997). Interacting phenotypes, or characters mediating social interactions, are unique because they can be both the targets and agents of selection (Moore et al. 1997, 1998). Moore et al. (1997) present a model of the quantitative genetics of interacting phenotypes. Here we present a complementary model of selection provided by and experienced by traits expressed in social interactions. Our model for selection makes no assumptions about the genetics of traits and therefore can be evaluated independent of the underlying genetics.

Social selection is thought to be a potent evolutionary force with dramatic consequences (West-Eberhard 1979, 1983, 1984). Behavior involved in interactions is widely thought to evolve more quickly than, and even lead the evolution of, other characters (Mayr 1963). Rapid and extreme divergence of social traits including social signals, ritualistic displays, competitive ability, altruism, and even inbreeding is predicted due to the runaway process that can be generated by social selection (West-Eberhard 1979, 1983, 1984; Breden and Wade 1991; Tanaka 1991, 1996). Interactions among relatives generate a specific form of social selection—kin selection (Hamilton 1964a; West-

Eberhard 1979). Seemingly maladaptive traits such as altruism can be understood through kin selection, where behaviors are both the agents of selection on relatives and the targets of selection provided by relatives (Hamilton 1964*a*, 1964*b*; Cheverud 1985; Queller 1985, 1992*a*, 1992*b*). In each of these cases, the strength of selection generated by social interactions is a key element to understanding how evolution proceeds.

Models of social evolution have traditionally combined both genetic parameters and selection measures into a single model (e.g., Hamilton 1964*a*, 1964*b*; Griffing 1981; Cheverud 1984, 1985; but see Queller 1985, 1992*a*, 1992*b*; Breden 1990; Frank 1995, 1997). These models have been successful in describing the evolution of social characters. However, their use by empirical biologists has been hampered because of the difficulty in estimating many of the critical parameters in these models (Grafen 1991; but see Griffing 1981, 1989; Heisler and Damuth 1987; Cheverud et al. 1988; Goodnight et al. 1992; Stevens et al. 1995). In contrast, approaches to understanding social evolution that have utilized Price's equation (1970, 1972; see also Queller 1985, 1992*a*, 1992*b*; Breden 1990; Frank 1995, 1997) have been able to partition fitness effects from genetics. These models rely on the relationship between regression and covariance to achieve this partitioning (for details, see Frank 1997). The separation of selection from genetics using Price's equation has been successfully applied to the study of ecologically important traits (Lande and Arnold 1983; Arnold and Wade 1984*a*). In contrast, social evolution models that allow for the separation of genetics from selection have been difficult to assess empirically. We present a model based on Price's equation that allows one to examine selection independently from genetics and that provides a framework in which social selection can be studied empirically.

The partitioning of selection and genetics has facilitated the study of character evolution because evolution is inherently a two-part process (Lande and Arnold 1983; Arnold 1994; Frank 1997). Selection acts to alter phenotypic distributions within generations, while inheritance allows for the cross-generational transmission of these changes (see Frank 1997). Selection can occur without an evolutionary response and, depending on the system of inheritance, the response to selection may not always be easily predicted from the measurement of selection. The separation of genetics from selection in the context of social evolution is likely to facilitate the empirical investigation of the evolution of interacting phenotypes because empirical measurements of selection and of genetic parameters are distinct processes (Stevens et al. 1995; Frank 1997). While there have been purely phenotypic studies of social interactions (i.e., studies that utilize the phenotypic gambit [*sensu* Grafen 1991]), few have produced

estimates of the force of social selection that can be used to model the evolution of interacting phenotypes when combined with the appropriate genetic model.

Social selection can be viewed as one component in the partitioning of selection (Arnold and Wade 1984*a*, 1984*b*; Frank 1997). When the characteristics of one individual affect the fitness of conspecifics, these interacting phenotypes (cf. Moore et al. 1997, 1998) become the agent of social selection. Variation in fitness associated with phenotypes expressed in social partners is then the opportunity for social selection. This component of fitness can be viewed distinctly from other components in the covariance approach to partitioning selection (Price 1970, 1972; Lande and Arnold 1983; Arnold and Wade 1984*a*, 1984*b*; Frank 1997). This approach is also analogous to and complements the contextual analysis models of selection (Heisler and Damuth 1987; Goodnight et al. 1992), where multilevel selection (e.g., group selection) is measured using a partial regression model that considers group structure or group level traits as a selective force.

In this article we present a model of social selection that achieves the separation of selection from genetics in the evolution of interacting phenotypes. Our model of social selection provides an empirical framework for measuring the force of social selection provided by and experienced by traits. The partitioning of factors affecting fitness allows for the separation of the force of social selection (i.e., selection provided by conspecifics; West-Eberhard 1979, 1983, 1984) from natural selection (i.e., ecological selection; West-Eberhard 1983). We use this approach to show the conditions under which variation in fitness generated by interactions among conspecifics is expected to result in a force of social selection acting on a particular trait. We show that the main factor generating social selection on traits is the phenotypic covariance among interacting individuals. Relatedness, as has been considered in kin selection models (which are a subset of the more general social selection models), is just one of many factors that can generate this covariance (Frank 1995). As with existing models of natural selection, our model can be combined with an appropriate genetic model (Moore et al. 1997, 1998) to model the evolution of social traits.

### A Model of Social Selection

Most theoretical treatments of the measurement of selection acting on traits have considered the direct relationship between traits expressed by an individual and that individual's fitness (Brodie et al. 1995; but see Frank 1997). However, factors other than one's own phenotype may affect an individual's fitness. Frank (1997) presents a general framework for modeling how variation in individual fitness can be attributed to any predictors that one wishes

to include in an analysis. Heisler and Damuth (1987; see also Goodnight et. al. 1992) present an analogous model where individual fitness is predicted by group-level traits (i.e., contextual traits). We present a simple model for social selection that is analogous to the approaches presented by Frank (1997), Queller (1985, 1992*a*, 1992*b*), and Heisler and Damuth (1987), where individual variation in fitness can be attributed to variation in the values of traits expressed by an individual's social partners (see also Cheverud 1985; Queller 1992*a*). We extend the standard regression approach of measuring selection to include an estimate of the strength of social selection, where an individual's fitness is, in part, determined by the characteristics of its social partners. This regression approach has been used by Queller (1985, 1992*a*, 1992*b*) and by Frank (1997) to analyze kin selection, where variation in fitness is partitioned into natural and kin selection. The regression approach to partitioning fitness allows one to estimate the effects of selection provided by social interactions that is independent of the effects of natural selection (i.e., the effects of the nonsocial environment on fitness). The partitioning of fitness effects in our model provides measures of both the selection experienced by traits (i.e., as targets) that is due to the social environment (i.e., social selection) and the degree to which particular traits generate a force of social selection (i.e., as agents) via their effects on the social environment.

#### *Fitness Effects of Social Interactions*

Lande and Arnold (1983) present a simple method for partitioning the independent effects that multiple traits have on individual fitness. In the multivariate model, they show that partial regression can be used to identify the independent effects that correlated traits have on fitness. While this method can be used to estimate the net selection gradient acting on a trait (when their assumptions are met), regression-based estimates combine the effects of natural and social selection. Arnold and Wade (1984*a*) extended Lande and Arnold's methods to examine selection acting in multiple episodes or through multiple fitness components (e.g., natural and sexual selection). While Arnold and Wade's method allows for the partitioning of selection into gradients associated with each episode of selection, as with Lande and Arnold (1983), this method implies that an individual's fitness is determined solely by its own phenotype. We extend this perspective to include situations, such as interacting phenotypes, where traits expressed by social partners affect an individual's fitness. We partition the effects of natural selection, as measured by the direct effect of a trait on an individual's fitness, from the effects of social selection, as measured by the effects

that traits expressed by an individual's social partners has on the fitness of the focal individual.

We denote the phenotype of the focal individual  $z_i$ , where the subscript  $i$  indicates the identity of the trait being measured in the focal individual. The phenotype of the individual's social partner is denoted  $z'_j$ , where the subscript  $j$  denotes the identity of the trait being measured in the social partner and the prime indicates that the trait is measured in a different individual (i.e., not in the focal individual). We assume that  $z_i$  and  $z'_j$  may represent either the same trait in both individuals (where  $i = j$ ) or may represent different traits in the two individuals (i.e.,  $i \neq j$ ). It is important to keep in mind that the traits  $z_i$  and  $z'_j$  are expressed in two different individuals, but fitness is measured for the focal individual (Grafen 1988; Queller 1992*a*, 1992*b*; Cheverud and Moore 1994). Thus, while it is necessary to measure all traits of the social environment (i.e., traits of all social partners) suspected to influence the fitness of focal individuals, it is not necessary to measure the fitness of all social partners unless they are also going to be considered focal individuals. For simplicity we assume that all phenotypic values are measured as deviations from the population mean (i.e., standardized to have a mean of zero).

In the case where an individual interacts with a single social partner, we partition effects on relative fitness ( $\omega$ ) as

$$\omega = \alpha + \beta_N z_i + \beta_S z'_j + \varepsilon, \quad (1)$$

where  $\beta_N$  is the natural selection gradient,  $\beta_S$  is the social selection gradient,  $\alpha$  is a constant (i.e., fitness that is uncorrelated with  $z_i$  or  $z'_j$ ; Phillips and Arnold 1989), and  $\varepsilon$  is an error term whose variance is to be minimized (Lande and Arnold 1983). We assume throughout that the residuals ( $\varepsilon$ ) are uncorrelated with the phenotypes being studied (i.e., represent random variation in fitness among individuals) and, thus, do not contribute to selection as considered here (for a discussion of this covariance see Queller 1992*a*). The natural selection gradient is defined as the partial regression of relative fitness on the value of a trait in the focal individual (Lande and Arnold 1983). The social selection gradient is defined as the partial regression of relative fitness in the focal individual on the value of trait  $z'_j$  expressed by its social partner (Queller 1992*a*, 1992*b*). As with all applications of partial regression, the correct assignment of social and natural selection gradients will depend on the correct identification and measurement of all factors that contribute to variance in fitness (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987; Grafen 1988; Schluter 1988).

This simple case, with just two traits, can be extended

to include the effects of multiple traits in the social partner on the fitness of the focal individual:

$$\omega = \alpha + \beta_N z_i + \sum_{j=1}^t \beta_{S_j} z'_j + \varepsilon, \quad (2)$$

where  $t$  is the number of traits being considered in the social partner. In this case, each of the social selection gradients ( $\beta_{S_j}$ , where the  $j$  indicates the identity of the trait in the social partner) measures the independent effect that a trait in one individual has on the fitness of its social partner.

We can extend equation (1) to include multiple social partners:

$$\omega = \alpha + \beta_N z_i + \beta_S \sum_{k=1}^n \frac{z'_{jk}}{n} + \varepsilon, \quad (3)$$

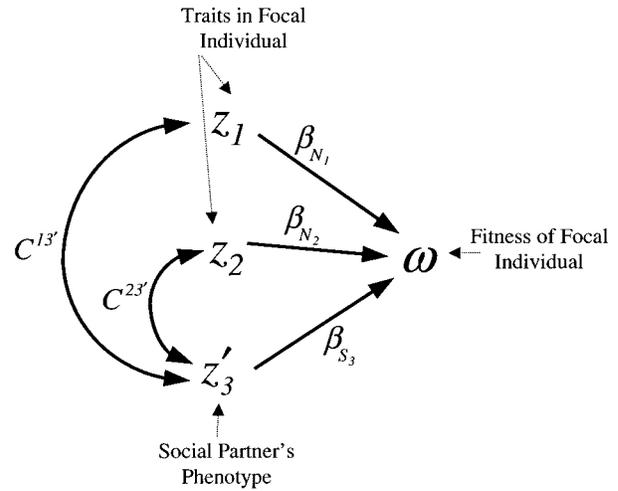
where the subscript  $k$  denotes the identity of the social partner and  $n$  gives the number of individuals with whom an individual interacts. The summation term gives the mean value for trait  $z'_j$  expressed by an individual's social partners. As before, the social selection gradient in this case identifies the effect that the social environment has on an individual's fitness, but now the gradient describes the effect of the mean environment experienced (Heisler and Damuth 1987). Assuming that each social encounter has an independent effect on fitness and that fitness is multiplicative (see Arnold and Wade 1984a for a discussion of this assumption), one can also partition these terms into selection gradients associated with each episode of selection (Arnold and Wade 1984a).

In the most general case, we can partition the fitness effects of multiple traits in the focal individual and multiple traits measured in multiple social partners:

$$\omega = \alpha + \sum_{i=1}^f \beta_{N_i} z_i + \sum_{j=1}^t \beta_{S_j} \sum_{k=1}^n \frac{z'_{jk}}{n} + \varepsilon, \quad (4)$$

where  $f$  is the number of traits being measured in the focal individual and the gradient  $\beta_{N_i}$  is the natural selection gradient associated with trait  $z_i$  (see fig. 1 for an example). The scenario described by equation (1) is equivalent to this general case where  $f$ ,  $n$ , and  $t$  are each equal to one. Similarly, each of the other previous equations can be derived from equation (4) by setting two of the three variables ( $f$ ,  $n$ , and  $t$ ) equal to 1.

The methods used for the empirical estimation of social and natural selection gradients are analogous to the standard methods used to measure selection in natural populations (see Brodie et al. 1995). However, interpretation of social selection gradients is fundamentally different than



**Figure 1:** Effects on individual fitness ( $\omega$ ). The fitness of the focal individual is affected by traits possessed by that individual ( $z_1$  and  $z_2$ ) and by trait  $z_3$  expressed by the individual's social partner. Natural selection gradients ( $\beta_{N_1}$  and  $\beta_{N_2}$ ) indicate the effect that the individual's traits have on its fitness, while the social selection gradient ( $\beta_{S_3}$ ) indicates the effect that trait  $z'_3$  expressed in the social partner has on the focal individual's fitness. The covariance between trait  $z_1$  in the focal individual and trait  $z'_3$  in the individual's social partner is labeled  $C^{13'}$ , while the covariance between  $z_2$  in the focal individual and  $z'_3$  in the social partner is  $C^{23'}$ .

that of natural selection gradients. Natural selection gradients that result from our partitioning of fitness describe the relationship between a trait and fitness resulting from ecological factors plus social factors that are not accounted for (e.g., due to characteristics of the social environment that are not measured). In contrast, social selection gradients ( $\beta_{S_j}$ ) measure the degree to which individual fitness varies as a function of interacting with individuals expressing a given value of some trait,  $z_i$ . Thus, despite the fact that traits  $z_i$  and  $z'_j$  are traits expressed in different individuals, they both affect the fitness of a single individual.

Nonlinear terms can be easily incorporated into these selection equations to account for curvature in the phenotype-fitness relationship (Phillips and Arnold 1989; Brodie et al. 1995). For example, quadratic terms can be added to estimate curvature that may exist in the fitness function as a result of nonlinear selection (Lande and Arnold 1983; Phillips and Arnold 1989). Interaction terms where fitness depends on the combination of traits possessed by an individual (as in epistatic or correlational selection; Lande and Arnold 1983; Phillips and Arnold 1989; Brodie 1992) or on the combination of traits expressed by the interacting individuals (see app. A) can also be included.

*Selection Resulting from Social Interactions*

While the partitioning of fitness shown in equations (1)–(4) can be used to account for variation in fitness among individuals, it does not, by itself, indicate the net force of selection that is experienced by a particular trait. The social selection gradient identifies the degree to which a trait expressed in one individual affects the fitness of other individuals. A nonzero value for  $\beta_s$  implies that the opportunity for social selection exists (cf. Crow 1958; West-Eberhard 1979, 1983, 1984) because it indicates that characteristics of the social environment (i.e., traits expressed in social partners) produce variance in fitness. However, this variance in fitness does not necessarily result in traits experiencing a net force of social selection. When there is no predictable relationship between the value of a trait expressed and the social environment experienced (i.e., when interactants are random with respect to trait values), social selection does not result despite the opportunity for social selection. For a particular trait to experience social selection, that trait must covary with the fitness effects attributable to the social interaction. This covariance view of selection (where selection is defined as the covariance of trait values with fitness) was derived by Price (1970, 1972; Breden 1990; Frank 1995, 1997). Using Price's equation, we define selection as

$$s_i = \text{cov}(z_i, \omega). \quad (5)$$

Price's equation allows us to take equation (1) and determine the conditions under which the opportunity for social selection results in social selection affecting specific characters. Recent analyses of Price's equation (Frank 1995, 1997) have demonstrated the value in partitioning selection from transmission (i.e., inheritance) through the covariance approach. Using this general framework, Frank discusses factors that may provide a force of selection (i.e., are "predictors of fitness"; Frank 1997, p. 1714). One advantage of this approach is the ability to examine any predictors of fitness (including social factors; e.g., Frank 1997). In the case presented here, we explore the consequences of social partners being those predictors of fitness.

When net selection gradients are measured (i.e., social and natural selection are not partitioned), the force of selection is calculated from the partial regression of individual trait values on fitness by taking the covariance of the trait,  $z_i$ , with relative fitness,  $\omega$  (Lande and Arnold 1983). In the simplest case, where only traits in the focal individual are measured, Price's equation produces the familiar equation for the selection differential (Lande and Arnold 1983):

$$s_i = \text{cov}(z_i, z_i)\beta_i = P_{ii}\beta_i, \quad (6)$$

where  $s_i$  is the selection differential, defined as the difference between the trait mean before and after selection ( $s_i = \bar{z}_i^* - \bar{z}_i$ , where the asterisk denotes the value measured after selection),  $\beta_i$  is the net selection gradient that includes the force of both natural and social selection (i.e., is the total regression of the trait on fitness), and  $P_{ii}$  is the phenotypic variance of trait  $z_i$  (i.e., the  $\text{cov}[z_i, z_i]$ ). The derivation of equation (6) assumes that the fitness residuals ( $\varepsilon$ ) are uncorrelated with the phenotype (i.e.,  $\text{cov}[z_i, \varepsilon]$  is zero). In addition, the  $\text{cov}[\alpha, \omega]$  is zero because  $\alpha$  is a constant.

When the fitness consequences of social partners are considered, we can partition selection into differentials due to the force of natural and social selection by taking the covariance of the trait value ( $z_i$ ) with fitness ( $\omega$ ) in equation (1):

$$s_i = P_{ii}\beta_N + \text{cov}(z_i, z'_j)\beta_S. \quad (7)$$

The first term,  $P_{ii}\beta_N$ , corresponds to the natural selection differential. The second term,  $\text{cov}(z_i, z'_j)\beta_S$ , is a measure of the force of social selection acting on trait  $z_i$  provided by trait  $z_j$  in a social partner. The covariance term,  $\text{cov}(z_i, z'_j)$ , accounts for the association between the selective environment provided by trait  $z_j$  with the trait  $z_i$  or, in other words, the covariance between the trait that acts as the agent of social selection and the trait that is the target of social selection. Again, we assume that the fitness residuals ( $\varepsilon$ ) are uncorrelated with the phenotype and thus do not contribute to selection. We denote the covariance between phenotypes of the interactants ( $\text{cov}[z_i, z'_j]$ , henceforth referred to as the covariance of interacting phenotypes) as  $C^{ij}$ , where the  $i$  denotes the identity of the trait being considered in the focal individual and  $j$  denotes the identity of the trait expressed by its social partners (see path in fig. 1). When this covariance is zero ( $C^{ij} = 0$ ), the trait  $z_j$  provides no net force of selection on trait  $z_i$  since the fitness effects attributed to trait  $z_j$  are experienced at random with respect to the value of trait  $z_i$ . However, when this covariance is nonzero (and  $\beta_S$  is nonzero), then the trait  $z_j$  provides a net force of social selection on trait  $z_i$ . For the simple two-trait case shown in equation (7), the selection differential can be expressed as

$$s_i = P_{ii}\beta_N + C^{ij}\beta_S. \quad (8)$$

The inclusion of the social selection term ( $C^{ij}\beta_S$ ) provides information that can be used to estimate the fitness consequences of social interactions separately from the effects of natural selection (see fig. 1). This covariance view of social selection based on Price's equation has been applied

to the problem of kin selection and is fundamentally equivalent to Hamilton's (1970) reformulation of kin selection in terms of covariance (Frank 1995).

When an individual interacts with multiple social partners, the covariance of interacting phenotypes measures the association between the phenotype of an individual and the mean value of the social environment experienced by that individual:

$$s_i = \text{cov}(z_i, z_i)\beta_N + \text{cov}(z_i, \bar{z}_j)\beta_s, \quad (9)$$

A similar extension can be made to include multiple traits measured in the social partner (i.e.,  $j$  takes on multiple values). With multiple traits measured in the social partner, the selection differential is

$$s_i = P_{ii}\beta_N + \sum_{j=1}^t C^{ij}\beta_s, \quad (10)$$

Equations (9) and (10) can be combined to include any number of traits and any number of social partners. The multivariate formulation can be expressed in matrix notation as

$$\mathbf{s} = \mathbf{P}\beta_N + \mathbf{C}^1\beta_s, \quad (11)$$

where  $\mathbf{s}$  is the vector of selection differentials (i.e.,  $\mathbf{s} = [s_1, s_2, s_3, \dots, s_f]$ ), where  $f$  is the number of traits in the focal individual being considered,  $\mathbf{P}$  is the phenotypic variance-covariance matrix with dimensions  $f \times f$ ,  $\beta_N$  is the vector of natural selection gradients (i.e.,  $\beta_N = [\beta_{N_1}, \beta_{N_2}, \beta_{N_3}, \dots, \beta_{N_f}]$ ),  $\mathbf{C}^1$  is the matrix of interactant phenotypic covariances and  $\beta_s$  is a vector of social selection gradients. The vector  $\beta_s$  has  $t$  elements, and  $\mathbf{C}^1$  is an  $f \times t$  matrix, where  $t$  is the number of traits measured in the social partners (i.e., values of the social environment). The elements of the matrix  $\mathbf{C}^1$  are the covariance of the focal individual phenotype (the rows) with the mean social environment (the columns) experienced by that individual. In general, the social environment can be taken as any factor created by conspecifics that affects the focal individual's fitness (see Frank 1997 for a discussion). The elements of  $\mathbf{C}^1$  can be measured as the covariance of the phenotypes of pairs of interacting individuals (if individuals interact in dyads) or as the covariance of the focal individual's phenotype with the mean phenotype of all of its social partners. The resulting composite selection differential,  $\mathbf{s}$ , can be used to predict changes in phenotypic values using standard quantitative genetic models (Roff 1997; Moore et al. 1997, 1998).

The partial regression formulation of social selection presented in equation (11) assumes that the effect of an

individual's phenotype on fitness is independent of the phenotype of its social partner. Likewise, the effect that the social partner's phenotype has on the fitness of the focal individual is independent of the phenotype of the focal individual. While this scenario is often assumed or implied in social selection models (see Queller 1992a for a review), the two effects actually may be nonindependent. Nonadditive or epistatic effects on fitness have been analyzed for inclusive fitness and kin selection (Queller 1985, 1992a) and are discussed in the context of our model in appendix A.

### The Covariance of Interacting Phenotypes

When social interactions determine (at least in part) an individual's fitness, the covariance of interacting phenotypes determines whether and how strongly a particular trait experiences social selection (West-Eberhard 1979, 1983, 1984). Many of the factors that contribute to covariance of interacting phenotypes have been considered separately as important factors in social selection. For example, relatedness (e.g., Hamilton 1964a, 1964b; Cheverud 1984, 1985), inbreeding (e.g., Breden and Wade 1981; Wade and Breden 1981), assortative interactions (e.g., Wilson and Dugatkin 1997), behavioral modification (Queller 1985), and indirect genetic effects (Kirkpatrick and Lande 1989; Moore et al. 1997, 1998; Wolf et al. 1998) are all expected to increase the phenotypic covariance between interactants. Understanding the diversity of factors that generate this covariance ( $C^{ij}$ ) is one key to understanding social selection.

*Nonrandom Interactions.* The simplest and most common factor that can generate a covariance of interacting phenotypes is nonrandom interaction. When individuals with particular traits seek out social partners based on their phenotypes (e.g., body size, color pattern), or some other factors result in associations of individuals based on their phenotype (e.g., habitat preferences), then we expect there to be a covariance between the interactants' phenotypes (Wilson and Dugatkin 1997). The most obvious example of this would be mechanisms and behavior resulting in sexual selection. However, associations of organisms into groups such as plant stands, bird flocks, insect swarms, mammal herds, or fish schools are common in nature (Wynne-Edwards 1962; Tinbergen 1966; Barbour et al. 1987), and any factors that result in nonrandom associations during the formation of such groups can potentially promote social selection by producing a covariance between the phenotypes of interacting individuals (Wilson and Dugatkin 1997). While these sources of nonrandom interactions may be common in nature, selection may fa-

vor the evolution of factors that either break up or reinforce nonrandom associations, making their role in the long-term evolution of social characters difficult to predict.

Factors such as habitat preference or other resource-use preferences can bias the phenotypic distribution of interactants. For example, if individuals assort nonrandomly on host plants, then traits that contribute to host-plant choice of individuals (e.g., chemosensory structures or feeding structures) or any traits correlated to these are expected to covary between individuals on the plant. Social selection, occurring as a result of competition for resources on the host plant, may be strong owing to the potentially large covariance of interacting phenotypes on the host plant. Social selection resulting from this process could potentially be a driving force in the evolution of competitive interactions.

Scenarios for the evolution of altruistic traits also provide an example where we might expect a positive value for  $C^{ij}$  to arise from nonrandom association. If altruistic individuals are able to seek out other altruistic individuals (or when individuals are able to seek out individuals that show a similar degree of altruistic behavior), a covariance between the altruism of the interactants will result. This situation might occur when individuals are able to predict the behavior of their potential social partners based on traits that indicate their likelihood to behave a certain way (e.g., as in green beard models; Dawkins 1976) or if individuals use past experiences to determine with whom to interact. In this case we can use the formulation of Hamilton's rule in appendix B to show that as long as individuals are able to accurately seek out individuals showing a similar degree of altruism (i.e.,  $C^{ij}$  is positive), then altruism may evolve, even with an associated cost (i.e.,  $\beta_N < 0$ ).

*Behavioral Modification.* Individuals sometimes alter their behavior based on the behavior of their social partners. This behavioral modification can generate a covariance between the phenotypes of the interactants. The sign and strength of this relationship depends, of course, on the nature of modification. When behavioral modification results in a positive interactant phenotypic covariance, the evolution of altruistic traits may be more likely (Queller 1985). Other examples include social dominance and territoriality, where one individual adopts a role of dominant while the other is subordinate.

Both empiricists and theoreticians have examined how behavioral modifications arise within stable social interactions (Huntingford and Turner 1987; Pusey and Packer 1997). Game theoretical approaches have been particularly influential in understanding how and why individuals may alter their actions based on the behavior of their social partner (Maynard Smith 1982). A familiar example is the

tit-for-tat strategy, where individuals play a strategy that allows them to avoid being cheated by their social partners (Axelrod and Hamilton 1981; see also Maynard Smith 1982). Because behavioral strategies such as tit-for-tat allow individuals to match the behavior of their partners, they can promote social selection for the same reasons that relatedness does—they produce positive covariance ( $C^{ij}$ ) between the traits of interactants.

*Relatedness, Inbreeding, and Kin Selection.* Relatedness among interactants is widely appreciated as generating social selection. The definition of social selection that we offer here places kin selection as a special case where individuals affect the fitness of their relatives (Cheverud 1984; Queller 1985, 1992a, 1992b; Lynch 1987). Relatedness is important simply because it produces a predictable covariance between the phenotypes of the interacting individuals. That is, because related individuals share genes, their phenotypes are expected to be similar, and thus a covariance should exist between the phenotypes of relatives. The phenotypic covariance of the same trait measured in relatives (i.e.,  $i = j$  in eq. [1]) can be expressed as

$$C^{ij} = rV_A + uV_D + r^2V_{A \times A} + ruV_{A \times D} + u^2V_{D \times D}, \quad (12)$$

where  $V_A$  is the additive genetic variance for the trait,  $V_D$  is the dominance variance,  $V_{A \times A}$  is the additive  $\times$  additive epistatic variance,  $V_{A \times D}$  is the additive  $\times$  dominance variance, and  $V_{D \times D}$  is the dominance  $\times$  dominance variance (assuming no maternal effects or environmental covariances; cf. chap. 9 in Falconer and Mackay 1996). The coefficient of relationship between the individuals,  $r$ , represents the probability that interacting individuals (i.e., relatives) share alleles that are identical by descent (Falconer and Mackay 1996). The coefficient  $u$  represents the probability that the interactants have the same genotype through identity by descent (for details and expected values of  $r$  and  $u$ , see Falconer and Mackay 1996; Lynch and Walsh 1998). The formulation in equation (12) ignores higher-order genetic interactions (i.e., ignores all interactions greater than two-way, such as  $V_{A \times A \times D}$ ) but can easily be generalized to include these additional terms (Falconer and Mackay 1996).

Equation (12) highlights the fact that, while dominance and epistasis do not contribute to the evolution of social characters (for examples, see Michod and Hamilton 1980; Seger 1981), these genetic factors can alter the way in which selection acts in social interactions. Because most models of kin selection combine selection with genetics to predict evolution, they correctly do not include dominance and epistasis. However, when one analyzes the selection component of social evolution, it is clear that dom-

inance and epistasis can contribute to social selection despite the fact that they do not contribute to the evolutionary response to selection. Equation (12) also points out another interesting feature of social selection; while it is possible to separate genetics from selection when studying evolution, genetics may play a role in determining how selection acts within the context of social interactions.

Previous analyses of social evolution have shown that inbreeding can facilitate the evolution of altruistic characters (e.g., Michod 1979; Wade and Breden 1981; Breden and Wade 1991). Our model of social selection identifies several modes through which inbreeding can facilitate altruistic evolution. When inbreeding occurs, the probability that related interactants share alleles that are identical by descent ( $r$ ) and the probability that individuals share genotypes that are identical by descent ( $u$ ) are increased (Lynch and Walsh 1998). However, inbreeding will only increase the covariance of the interacting phenotypes under certain circumstances. If an entire population is inbred, then the average covariance between relatives is not elevated because inbreeding has increased the phenotypic similarity among all pairs of individuals in the population. Alternatively, when lineages within a population are inbred, and if individuals interact with others from their lineage, then the covariance of interacting phenotypes will be elevated by inbreeding. In this case we would measure relatedness using  $F_{ST}$  (Wright 1969), where we are measuring the genetic similarity of interactants (the subpopulation) relative to the total population.

A full analytical description of the effects of inbreeding on the covariance between relatives is quite complex and is not presented here (for details see Harris 1964; Jacquard 1974; Lynch and Walsh 1998). As a simple example, consider offspring that result from a single generation of full-sib mating (i.e., the parents of the full sibs being mated were themselves not inbred). Inbreeding increases the value of  $r$  from 0.50 to a value of about 0.60 and increases  $u$  from 0.25 to about 0.28. As a result,  $C^{ij}$  will be larger than for outbred sibs. In addition, because inbreeding is expected to increase the value of  $u$ , it makes the epistatic and dominance effects of genes more important for resemblance of relatives and for social selection.

In addition to its affects on  $r$  and  $u$ , inbreeding is expected to affect genetic variance components. The additive genetic variance in a population is expected to increase with inbreeding, because of the redistribution of genetic variance from within to among related groups (e.g., genetic lines or demes; Falconer and Mackay 1996). Inbreeding can also affect the dominance or epistatic variance components in a similar way (Falconer and Mackay 1996; Crow and Kimura 1970). Thus, inbreeding may facilitate the evolution of social characters as a result of its combined effect on the probability of allelic and genotypic identity

by descent and on genetic variance (see also Breden and Wade 1991).

Most models of kin selection have been concerned with the conditions under which a trait that lowers an individual's fitness can evolve as a result of the effects that this trait has on the fitness of that individual's relatives. Restated in terms of our model, a kin selection model can be used to determine whether the force of selection provided by social selection outweighs the force of natural selection when they are in opposition. The conditions under which the balance of natural and social selection favors altruistic traits have traditionally been expressed using Hamilton's rule (Hamilton 1964a; Cheverud 1984, 1985). In appendix B we extend the kin selection formulation of Hamilton's rule to include all socially selected traits. We show that the conditions stated in Hamilton's rule (and in quantitative genetic reformulations of the rule; Cheverud 1984, 1985; Queller 1985, 1992a, 1992b; Cheverud and Moore 1994) can be applied to any type of social interaction, where the covariance of interacting phenotypes replaces the usual measure of genetic relatedness.

Considerations of kin selection are often equated with considerations of inclusive fitness (Queller 1992a, 1992b). As with standard measures of selection (e.g., Lande and Arnold 1983), our partitioning of fitness works for cases where all individuals exhibit a particular trait. In many cases, we are interested in social traits that are not expressed by all individuals (e.g., sex-limited traits). When some individuals do not express a trait, it may be difficult to estimate the total covariance between the genotype and fitness. This total covariance is important because it determines the evolutionary response to selection (see Frank 1997). When factors such as kinship produce a covariance between the genotype and fitness that cannot be accounted for by the covariance between the phenotype and fitness, then it may be difficult to predict evolution. This problem can be alleviated if one can estimate the total covariance between the genotype and fitness. This can be achieved by using an approach that considers inclusive fitness (Queller 1992a). The inclusive fitness approach allows one to predict evolution by considering the covariance between the genotype of an individual and the social environment experienced (i.e., the partner's phenotype). For a detailed discussion of quantitative genetic social selection models for inclusive fitness see Queller (1992a, 1992b) and Frank (1997).

*Indirect Genetic Effects.* Indirect genetic effects can also generate covariation between the phenotypes of interacting individuals in a way similar to behavioral modification (Kirkpatrick and Lande 1989; Moore et al. 1997, 1998). Indirect genetic effects occur when genes expressed in one

individual have phenotypic effects on another individual (Moore et al. 1997, 1998; Wolf et al. 1998). Thus, behavioral modification may be seen as a subset of indirect genetic effects when the behavior is heritable. Examples of traits potentially influenced by indirect genetic effects include plant height (influenced by height of neighboring plants and induced by shade avoidance; Smith and Whitelam 1997) and the expression of behavioral aggression in chickens (Muir 1996). Moore et al. (1997, 1998) provide a more extensive list of the role of indirect genetic effects in social behavior.

Indirect genetic effects have been modeled for interactions among both related and unrelated individuals (Kirkpatrick and Lande 1989; Moore et al. 1997, 1998; Wolf et al. 1998). As an example, we consider the simple case where a single trait affects the expression of the same trait in another, unrelated, individual in a pairwise interaction (after eq. 13 in Moore et al. 1997):

$$z_1 = a_1 + e_1 + \psi z'_1, \quad (13)$$

where  $z_1$  and  $z'_1$  denote the phenotypic value of trait 1 expressed in the focal individual and its social partner, respectively,  $a_1$  is the additive genetic component, and  $e_1$  is the environmental component (see fig. 2). The coefficient  $\psi$  is a measure of the degree to which the expression of trait  $z_1$  in the focal individual is influenced by the expression of trait  $z_1$  in its social partner (see Moore et al. 1997 for the complete model). Using equation (13), we can derive the expected covariance between the interacting phenotypes when interactions occur at random. In the case of a single trait  $C^{ij}$  can be expressed as  $C^{i'j'}$  (where both  $i$  and  $j$  are 1)

$$C^{i'j'} = \frac{2\psi V_A}{(1 - \psi^2)^2}, \quad (14)$$

where  $V_A$  is the additive genetic variance of trait  $z_1$ . Thus, even when individuals interact at random, indirect genetic effects create a covariance between the phenotypes of the interactants. When  $\psi$  is negative (i.e.,  $z_1$  negatively affects the expression of the same trait in the social partner), then the phenotypes of the interactants are dissimilar and the covariance produced is negative. Conversely, when  $\psi$  is positive,  $C^{i'j'}$  is positive, and indirect genetic effects result in the phenotypes of the interactants being similar.

Indirect genetic effects have often been considered in the mother-offspring interaction, where the maternal phenotype affects the expression of the offspring phenotype (i.e., maternal effects occur). An approach similar to the one we use here was first used to consider the effect of the maternal phenotype on offspring fitness (i.e., maternal selection, see eq. 11 in Kirkpatrick and Lande 1989). In

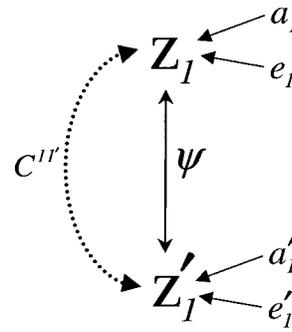


Figure 2: Pathway of indirect genetic effects. Trait  $z_1$  is affected by expression of trait  $z_1$  in a social partner (whose phenotype is indicated with a prime). The coefficient  $\psi$  measures the degree to which trait  $z_1$  is affected by the phenotype of the social partner. The  $C^{i'j'}$  measures the covariance between the phenotypes of the interactants. The  $a_1$  represents the additive genetic component of the phenotype, and  $e_1$  represents the random environmental component of the phenotype. Primes are used to indicate components of the phenotype expressed in the social partner.

their analysis of maternal effects, Kirkpatrick and Lande derived an equation for the covariance between the maternal and offspring phenotypes (eq. A8 in Kirkpatrick and Lande 1989) that is equivalent to our interacting phenotype covariance ( $C^{ij}$  or  $C^{i'j'}$ ). Their model shows that with maternal effects present, the phenotypic covariance between mother and offspring may be greater or less than expected based on genetic similarity between the two. Maternal effects can also increase the phenotypic similarity between sibs beyond the degree predicted based on their genetic similarity. Thus, indirect genetic effects are expected to be a generally important source of phenotypic resemblance between interactants. When combined with appropriate genetic models, an indirect genetic effect approach can be used to model evolution by kin selection (e.g., Cheverud 1984), group selection (Cheverud 1985), and social selection (Moore et al. 1997, 1998).

### Discussion

When the social environment generates variance in fitness the opportunity for social selection exists (sensu Crow 1958). As with ordinary traits, the opportunity for selection is a requisite for selection to occur, but does not necessarily imply that any particular trait experiences selection. Characters experience selection only when they covary with fitness (see Price 1970, 1972; Breden 1990). Our model illustrates that when the variation in fitness

owing to the social environment can be attributed to particular characteristics of the social environment, then social selection gradients can exist. When social selection gradients exist, fitness is determined in part by the traits of social partners, so it is the covariance between an individual's traits and its partners' traits (i.e., the covariance of interacting phenotypes,  $C^{ij}$ ) that describes how variance in fitness created by the social environment results in social selection.

Because it is the covariance of interacting phenotypes that determines when social selection acts on any particular trait, any factor that contributes to a correlation among characteristics of interactants can promote social selection. Factors such as relatedness, assortative interactions, behavioral modification, and indirect genetic effects can all result in a predictable covariance between the traits expressed by social partners. Our partitioning of fitness shows that these seemingly disparate factors that generate covariance between a trait providing social selection and the traits experiencing social selection can be unified into a single framework. Thus, our model supports West-Eberhard's (1979, 1983) suggestion that there is no fundamental difference between sexual selection, kin selection, and other forms of social selection.

As a purely phenotypic formulation of selection, the data necessary to measure social selection are readily observable without the added difficulty of discerning relatedness of interactants or the measurement of genetic parameters. When genetics, especially those of interacting phenotypes (Moore et al. 1997, 1998), can be measured in a system, they can be combined with the estimates of social selection to model the short-term and potentially long-term evolution of social characters in a system in the same manor as standard quantitative genetic models of evolution. Even when genetic information is not available, consideration of the specific factors contributing to and experiencing social selection can still be analyzed and should provide insight into the process of social evolution.

#### Acknowledgments

We thank A. F. Agrawal, J. M. Cheverud, C. J. Goodnight, P. X. Kover, A. Sih, M. J. Wade, M. J. West-Eberhard, and D. F. Westneat for insightful discussions during the development of these ideas. Thanks to F. J. Breden, M. A. McPeck, and an anonymous reviewer for their thoughtful comments on the manuscript. This research was supported by the NSF Graduate Research Fellowship (DGE-9355093) and a University of Kentucky Fellowship to J.B.W.; NSF IBN-9514063, DEB-9521821, and IBN-9616203; as well as State and Federal

Hatch support to A.J.M.; and IBN-9896116 to E.D.B. III.

## APPENDIX A

### Nonadditive Effects

While traits may independently affect an individual's fitness, traits may also interact in such a way that fitness depends on the combination of traits expressed (i.e., epistatic or correlational selection; Olson and Miller 1958; Lande and Arnold 1983; Phillips and Arnold 1989; Brodie 1992). Similarly, the effect that a trait expressed in one individual has on fitness may depend on the traits expressed by that individual's social partners and vice versa (e.g., traits may have synergistic effects on fitness; Cheverud 1985; Queller 1985). One can account for this type of interaction between individual traits and the social environment by adding an interaction term to our model of fitness (Cheverud 1985; Queller 1985). When trait  $z_i$  is heritable, this term can be thought of as a genotype  $\times$  environment interaction for fitness, where the genes for trait  $z_i$  interact with the social environment provided by trait  $z'_j$  to determine fitness.

Adding an interaction term to equation (1) we get

$$\omega = \alpha + \beta_N z_i + \beta_S z'_j + \beta_I z_i z'_j + \varepsilon, \quad (A1)$$

where  $\beta_I$  is the nonadditive social selection gradient (i.e., deviation from additivity [Queller 1985] or synergism coefficient [Queller 1992a]). This coefficient measures the degree to which the phenotypes of the two individuals interact to determine the fitness of the focal individual. In other words, we can view the natural selection gradient ( $\beta_N$ ) as the main effect of trait  $z_i$  on an individual's fitness; the social selection gradient ( $\beta_S$ ) as the main effect of trait  $z_j$  expressed by a social partner on the fitness of the focal individual; and the nonadditive social gradient ( $\beta_I$ ) as the interaction between traits  $z_i$  (a trait in the focal individual) and  $z'_j$  (expressed by that individual's partners; cf. Lande and Arnold 1983; Queller 1985).

As in the case of additivity, we can derive an equation for the selection coefficient by taking the covariance of the trait,  $z_i$ , with fitness,  $\omega$  in equation (A1) (following Bohrenstedt and Goldberger 1969):

$$s = P_{ii} \beta_N + C^{ij} \beta_S + (\bar{z}_j P_{ii} + \bar{z}_i C^{ij}) \beta_I, \quad (A2)$$

where  $\bar{z}_i$  is the mean value of trait  $z_i$ , and  $\bar{z}_j$  is the mean value of trait  $z_j$ . We see that, as in the case of additive fitness effects, the covariance of interacting phenotypes is important in determining the degree to which a trait experiences a net force of social selection when fitness is

affected by interactions with conspecifics. We can also see that the interaction term is unlikely to contribute to a net selection differential since the last term in equation (A2) should equal 0 in most cases. This is because  $\bar{z}_i$  and  $\bar{z}_j$  are expected to be 0 given that trait values are measured as deviations from the mean.

## APPENDIX B

### General Formulation of Hamilton's Rule

Hamilton's rule (Hamilton 1964*a*) gives the conditions under which an altruistic trait, defined as a trait that increases the fitness of others at the expense of a decrease in an individual's own fitness, increases in frequency or value in a population. In its simplest formulation, Hamilton's rule states that in order for an altruistic trait to increase in frequency the fitness cost-to-benefit ratio must be greater than the coefficient of relatedness of the interactants. The conditions of Hamilton's rule have been extended by Cheverud (1984; Cheverud and Moore 1994; see also Wolf et al. 1998) and Queller (1985, 1992*a*, 1992*b*) to include traits with quantitative inheritance. These previous formulations of Hamilton's rule applied to the evolution of quantitative traits combined selection and genetics into a single equation. Here we provide a purely phenotypic formulation of Hamilton's rule that gives the conditions under which a social trait experiences net positive selection.

Assuming that both individuals express the same altruistic trait such that  $i = j$  in the definition of the phenotypes of the interactants in equation (1),  $\beta_N$  measures the natural selection cost of being altruistic (i.e.,  $\beta_N < 0$ ), and  $\beta_S$  measures the benefit to the social partner (i.e.,  $\beta_S > 0$ ), then a similar extension can be accomplished by stating the conditions under which the net selection differential,  $s_p$ , in equation (8) is greater than 0:

$$\frac{C^{ij'}}{P_{ii}}\beta_S + \beta_N > 0. \quad (\text{B1})$$

The natural selection gradient is used as a measure of the fitness cost of being altruistic because, by definition, it describes the decrease in fitness of the focal individual that results from a unit increase in the value of the altruistic trait ( $z_i$ ). Likewise, the social selection gradient measures the benefit because it describes the increase in the fitness of the focal individual due to a unit increase in value of the altruistic trait expressed by that individual's social partners ( $z_j$ ).

The formulation in equation (B1) can be rearranged to identify the conditions under which the benefit of per-

forming an altruistic behavior outweighs the cost associated with performing the behavior:

$$\frac{C^{ij'}}{P_{ii}} > -\frac{\beta_N}{\beta_S}. \quad (\text{B2})$$

From this equation it is clear that the conditions under which net selection on an altruistic trait is positive require that the magnitude of the cost-to-benefit ratio must be greater than the ratio of the phenotypic covariance between the interactants to the variance of the trait  $z_i$ . The latter term, the ratio of phenotypic resemblance (as measured by  $C^{ij'}$ ) to the phenotypic variance, will be equivalent to the coefficient of relatedness when traits show Mendelian inheritance with additive genetic effects (Falconer and Mackay 1996). This formulation points out that, contrary to Hamilton's original formulation (1964*a*), identity by descent is not necessarily important for social evolution (Hamilton 1970; Queller 1985; Frank 1995).

While equations (B1) and (B2) give the conditions under which the trait  $z_i$  experiences positive net selection, it cannot be used on its own to predict the response to selection of an altruistic trait. The conditions under which a trait experiences positive net selection must be combined with a response to selection model (i.e., a model of inheritance) to find the conditions under which the response to selection of an altruistic trait is positive (Cheverud 1984; Queller 1985, 1992*a*, 1992*b*; Cheverud and Moore 1994; Wolf et al. 1998). This points out the value of separating fitness measures (i.e., selection) from genetics (i.e., determinants of the response to selection; Cheverud and Moore 1994) when modeling evolution. Under most conditions, the direction of the selection gradients and the direction of the evolutionary response to selection will be the same, making the selection gradient adequate to understand the direction of evolution. However, under some limited conditions, such as when maternal effects exist, the covariance between the genotype and phenotype being studied may actually be negative (see Cheverud 1985; Wolf et al. 1998), making the direction of selection and response to selection opposite in sign.

When our formulation of Hamilton's rule is compared with previous versions (e.g., Hamilton 1964*a*; Cheverud 1984; Cheverud and Moore 1994), we find that there are actually two Hamilton's rules that must both be satisfied in order for an altruistic trait to increase in value. The first Hamilton's rule (i.e., the one presented here) can be used to identify the conditions under which the net selection acting on a social trait (i.e., an altruistic trait) is positive or negative. The second Hamilton's rule gives the conditions under which the response to social selection is expected to be positive or negative. This latter set of conditions will depend on factors such as the mapping of the

phenotype to the genotype and the strength of selection on correlated characters. Despite the requirement that both rules be met, the purely phenotypic Hamilton's rule should prove to be useful in most systems because the conditions under which the rule fails to predict the direction of evolution are very limited.

#### Literature Cited

- Arnold, S. J. 1994. Multivariate inheritance and evolution: a review of the concepts. Pages 17–48 in C. R. B. Boake, ed. *Quantitative genetic studies of behavioral evolution*. University of Chicago Press, Chicago.
- Arnold, S. J., and M. J. Wade. 1984a. On the measurement of natural and sexual selection: theory. *Evolution* 38:709–719.
- . 1984b. On the measurement of natural and sexual selection: applications. *Evolution* 38:720–734.
- Axelrod, R., and W. D. Hamilton. 1981. The evolution of cooperation. *Science* 211:1390–1396.
- Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. *Terrestrial plant ecology*. 2d ed. Benjamin-Cummings, Menlo Park, Calif.
- Bohrenstedt, G. W., and A. S. Goldberger. 1969. On the exact covariance of products of random variables. *Journal of the American Statistical Association* 64:1439–1442.
- Breden, F. 1990. Partitioning of covariance as a method for studying kin selection. *Trends in Ecology & Evolution* 5:224–228.
- Breden, F. J., and M. J. Wade. 1981. Inbreeding and evolution by kin selection. *Ethology and Sociobiology* 2:3–16.
- . 1991. “Runaway” social evolution: reinforcing selection of inbreeding and altruism. *Journal of Theoretical Biology* 153:323–337.
- Brodie, E. D., III. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution* 46:1284–1298.
- Brodie, E. D., III, A. J. Moore, and F. J. Janzen. 1995. Visualizing and quantifying natural selection. *Trends in Ecology & Evolution* 10:313–318.
- Cheverud, J. M. 1984. Evolution by kin selection: a quantitative genetic model illustrated by maternal performance in mice. *Evolution* 38:766–77.
- . 1985. A quantitative genetic model of altruistic selection. *Behavioral Ecology and Sociobiology* 16:239–243.
- Cheverud, J. M., B. D. Chepko-Sade, M. M. Dow, and D. S. Sade. 1988. Group selection models with population substructure based on social interaction networks. *American Journal of Physical Anthropology* 77:427–433.
- Cheverud, J. M., and A. J. Moore. 1994. Quantitative genetics and the role of the environment provided by relatives in the evolution of behavior. Pages 67–100 in C. R. B. Boake, ed. *Quantitative genetic studies of behavioral evolution*. University of Chicago Press, Chicago.
- Crook, J. H. 1972. Sexual selection, dimorphism, and social organization in the primates. Pages 231–281 in B. Campbell, ed. *Sexual selection and the descent of man, 1871–1971*. Aldine, Chicago.
- Crow, J. F. 1958. Some possibilities for measuring selection intensities in man. *Human Biology* 30:1–13.
- Crow, J. F., and M. Kimura. 1970. *An introduction to population genetics theory*. Burgess, Minneapolis.
- Dawkins, R. 1976. *The selfish gene*. Oxford University Press, Oxford.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. 4th ed. Longman, Essex.
- Frank, S. A. 1995. George Price's contribution to evolutionary genetics. *Journal of Theoretical Biology* 175:373–388.
- . 1997. The Price equation, Fisher's fundamental theorem, kin selection and causal analysis. *Evolution* 51:1712–1729.
- Goodnight, C. J., J. M. Schwartz, and L. Stevens. 1992. Contextual analysis of models of group selection, soft selection, hard selection and the evolution of altruism. *American Naturalist* 140:743–761.
- Grafen, A. 1988. On the uses of data on lifetime reproductive success. Pages 454–471 in T. H. Clutton-Brock, ed. *Reproductive success*. University of Chicago Press, Chicago.
- . 1991. Modeling in behavioural ecology. Pages 5–31 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. 3d ed. Blackwell Scientific, Oxford.
- Griffing, B. 1981. A theory of natural selection incorporating interactions among individuals. I. The modeling process. *Journal of Theoretical Biology* 89:636–658.
- . 1989. Genetic analysis of plant mixtures. *Genetics* 122:943–956.
- Hamilton, W. D. 1964a. The genetical evolution of social behavior. I. *Journal of Theoretical Biology* 7:1–16.
- . 1964b. The genetical evolution of social behavior. II. *Journal of Theoretical Biology* 7:17–52.
- . 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature (London)* 228:1218–1220.
- Harris, D. L. 1964. Genotypic covariances between inbred relatives. *Genetics* 50:1319–1348.
- Heisler, I. L., and J. D. Damuth. 1987. A method for analyzing selection in hierarchically structured populations. *American Naturalist* 130:582–602.
- Huntingford, F., and A. K. Turner. 1987. *Animal conflict*. Chapman & Hall, New York.

- Jacquard, A. 1974. The genetic structure of populations. Springer, Berlin.
- Kirkpatrick, M., and R. Lande. 1989. The evolution of maternal characters. *Evolution* 43:485–503.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- Lynch, M. 1987. Evolution of intrafamilial interactions. *Proceedings of the National Academy of Sciences of the USA* 84:8507–8511.
- Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, Mass.
- Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.
- Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Mass.
- Michod, R. E. 1979. Genetical aspect of kin selection: effects of inbreeding. *Journal of Theoretical Biology* 81: 223–233.
- Michod, R. E., and W. D. Hamilton. 1980. Coefficients of relatedness and sociobiology. *Nature (London)* 288: 694–697.
- Mitchell-Olds, T., and R. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* 41:1149–1161.
- Moore, A. J., E. D. Brodie III, and J. B. Wolf. 1997. Interacting phenotypes and the evolutionary process. I. Direct and indirect genetic effects of social interactions. *Evolution* 51:1352–1362.
- Moore, A. J., J. B. Wolf, and E. D. Brodie III. 1998. The influence of direct and indirect genetic effects on the evolution of behavior: sexual and social selection meet maternal effects. Pages 22–41 in T. A. Mousseau and C. W. Fox, eds. *Maternal effects as adaptations*. Oxford University Press, Oxford.
- Muir, W. M. 1996. Group selection for adaptation to multiple-hen cages: selection program and direct responses. *Poultry Science* 75:447–458.
- Olson, E. C., and R. L. Miller 1958. Morphological integration. University of Chicago Press, Chicago.
- Phillips, P. C., and S. J. Arnold. 1989. Visualizing multivariate selection. *Evolution* 43:1209–1222.
- Price, G. R. 1970. Selection and covariance. *Nature (London)* 227:520–521.
- . 1972. Extension of covariance selection mathematics. *Annals of Human Genetics* 35:485–490.
- Pusey, A. E., and C. Packer. 1997. The ecology of relationships. Pages 254–283 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. 4th ed. Blackwell Science, London.
- Queller, D. C. 1985. Kinship, reciprocity and synergism in the evolution of social behavior. *Nature (London)* 318: 366–367.
- . 1992a. Quantitative genetics, inclusive fitness, and group selection. *American Naturalist* 139:540–558.
- . 1992b. A general model for kin selection. *Evolution* 46:376–380.
- Rice, E. L. 1984. *Allelopathy*. 2d ed. Academic Press, Orlando, Fla.
- Roff, D. A. 1997. *Evolutionary quantitative genetics*. Chapman & Hall, New York.
- Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution* 42:849–861.
- Seeger, J. 1981. Kinship and covariance. *Journal of Theoretical Biology* 91:191–213.
- Smith, H., and G. C. Whitelam. 1997. The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant Cell and Environment* 20:840–844.
- Stevens, L., C. J. Goodnight, and S. Kalisz. 1995. Multilevel selection in natural populations of jewelweed, *Impatiens capensis*. *American Naturalist* 145:513–526.
- Tanaka, Y. 1991. The evolution of social communication systems in a subdivided population. *Journal of Theoretical Biology* 149:145–163.
- . 1996. Social selection and the evolution of animal signals. *Evolution* 50:512–523.
- Tinbergen, N. 1966. *Social behaviour in animals with special reference to vertebrates*. Methuen, London.
- Wade, M. J., and F. J. Breden. 1981. The effect of inbreeding on the evolution of altruistic behavior by kin selection. *Evolution* 35:844–858.
- West-Eberhard, M. J. 1979. Sexual selection, social competition and evolution. *Proceedings of the American Philosophical Society* 123:222–234.
- . 1983. Sexual selection, social competition and speciation. *Quarterly Review of Biology* 58:155–183.
- . 1984. Sexual selection, competitive communication and species-specific signals. Pages 283–324 in T. Lewis, ed. *Insect communication*. Academic Press, New York.
- Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. *Nature (London)* 308:181–184.
- Wilson, D. S., and L. A. Dugatkin. 1997. Group selection and assortative interactions. *American Naturalist* 149: 336–351.
- Wright, S. 1969. *Evolution and the genetics of populations*. Vol. 2. The theory of gene frequencies. University of Chicago Press, Chicago.
- Wolf, J. B., E. D. Brodie III, J. M. Cheverud, A. J. Moore, and M. J. Wade. 1998. Evolutionary consequences of indirect genetic effects. *Trends in Ecology & Evolution* 13:64–69.
- Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver & Boyd, Edinburgh.