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INTERACTING PHENOTYPES AND THE EVOLUTIONARY PROCESS. III. SOCIAL EVOLUTION

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Interactions among conspecifics influence social evolution through two distinct but intimately related paths. First, they provide the opportunity for indirect genetic effects (IGEs), where genes expressed in one individual influence the expression of traits in others. Second, interactions can generate social selection when traits expressed in one individual influence the fitness of others. Here, we present a quantitative genetic model of multivariate trait evolution that integrates the effects of both IGEs and social selection, which have previously been modeled independently. We show that social selection affects evolutionary change whenever the breeding value of one individual covaries with the phenotype of its social partners. This covariance can be created by both relatedness and IGEs, which are shown to have parallel roles in determining evolutionary response. We show that social selection is central to the estimation of inclusive fitness and derive a version of Hamilton's rule showing the symmetrical effects of relatedness and IGEs on the evolution of altruism. We illustrate the utility of our approach using altruism, greenbeards, aggression, and weapons as examples. Our model provides a general predictive equation for the evolution of social phenotypes that encompasses specific cases such as kin selection and reciprocity. The parameters can be measured empirically, and we emphasize the importance of considering both IGEs and social selection, in addition to relatedness, when testing hypotheses about social evolution.

KEY WORDS: **Altruism, greenbeards, indirect genetic effects, kin selection, reciprocity, social selection.**

Evolution by natural selection can be modeled as two sequential processes: phenotypic selection, which leads to changes in the distribution of phenotypes within a generation, and inheritance, which translates these changes across generations (Fisher 1930; Lande 1979; Falconer and MacKay 1996). In the traditional view, fitness differences among individuals reflect responses to the physical environment, giving rise to selection favoring phenotypes appropriate to that environment. Evolutionary change then occurs when alleles associated with these favored phenotypes increase in frequency across generations. The relationships between genotype and phenotype and between phenotype and fitness are often more complex than this, however, and these intricacies may influence the rate and direction of phenotypic evolution (Dawkins 1982; Mousseau and Fox 1998; Wolf et al. 1998, 2000; Pigliucci 2001; Odling-Smee et al. 2003; West-Eberhard 2003; Lande 2009).

Traits involved in interactions among conspecifics are notable cases in which simple evolutionary models are inappropriate

(Darwin 1859; West-Eberhard 1979, 1983; Lande 1981; Frank 1998). In animals, such interactions typically involve social behavior, the study of which makes up much of the field of behavioral ecology (Székely et al. 2010; Westneat and Fox 2010). However, social interactions do not necessarily require an animal nervous system and occur in virtually all taxa (Frank 2007; e.g., microorganisms, Crespi 2001; Foster 2010; plants, Dicke et al. 2003; Karban 2008). Behavior such as aggression and courtship in animals are the most intuitive examples, but competitive interactions such as relative growth rates of neighboring plants exhibit the same kinds of phenotypic feedback (Mutic and Wolf 2007). Social effects on phenotypic evolution may occur whenever "interacting phenotypes" are present, that is, when the phenotype of one individual affects the phenotype or fitness of a conspecific (Moore et al. 1997; Wolf et al. 1998, 1999; Bleakley et al. 2010; Wolf and Moore 2010).

Social interactions moderate inheritance by altering the relationship between genotype and phenotype. For example, the behavior of a focal individual may depend on the behavior of its social partner(s) so that phenotypic expression is determined by both the individual's own genes and those of its social partner(s) (Fig. 1). The phenotypic effects of genes in social partners are known as "indirect genetic effects" (IGEs, Moore et al. 1997; Wolf et al. 1998; Wolf and Moore 2010) or associative genetic effects (Griffing 1967, 1969, 1976, 1981a; Bijma et al. 2007a; Bijma and Wade 2008). Because they are genetic in origin, IGEs represent an environmental source of variance that is heritable and thus contributes to the evolutionary response to selection.

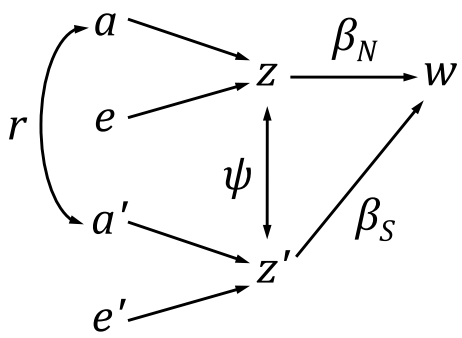

Figure 1. Path diagram depicting the effects of interacting phenotypes on phenotypic evolution. Variables associated with a focal individual are shown with no superscript, and variables associated with its interactant are given a prime. Each phenotype is affected by additive genetic (*a*), environmental (*e*), and indirect genetic effects. Relatedness between the two individuals is represented by the path coefficient *r*. The path coefficient ψ translates the interactant's phenotype into an indirect genetic effect, which is shown as a double arrow to indicate that the effect is reciprocal. The fitness of the focal individual (*w*) is affected by both its own phenotype (nonsocial selection, β_N) and that of its interactant (social selection, β_S).

Consequently, IGEs can alter the evolutionary dynamics of traits compared to those expected under traditional quantitative genetic models (Moore et al. 1997).

Social interactions affect selection by directly generating fitness differences among individuals. This path is termed social selection, which is broadly defined to include any case in which conspecific interactions lead to variance in reproductive success, including competition, cooperation, and sexual selection (Darwin 1859; Wynne-Edwards 1962; Crook 1972; West-Eberhard 1979, 1983; Frank 2006). Although this perspective captures the range of relevant interactions, it does not provide a means to distinguish social selection from nonsocial selection in a quantitative way. Wolf et al. (1999) narrowed the definition by explicitly recognizing social selection as effects on the fitness of one individual that directly result from traits of interacting individuals. There are at least three advantages to adopting this definition of social selection. First, social selection can be measured using standard and widely used multiple regression techniques that have been used to generate a wealth of data on individual-level selection (Lande and Arnold 1983; Kingsolver et al. 2001). This approach measures social selection as the effect of social-partner or group traits on the fitness of a focal individual, while controlling for the effects of that individual's own traits (as in contextual analysis, Heisler and Damuth 1987; Goodnight et al. 1992). Second, the accounting of fitness is individual based and remains consistent across all individuals in the population. The individual fitness approach yields equivalent results to inclusive and multilevel fitness formulation when appropriate assumptions are made (Queller 1992a; Frank 1998; Taylor et al. 2007; Bijma and Wade 2008). Third, selection gradients can be combined with quantitative genetic parameters to predict evolutionary response to selection (Lande 1979; Lande and Arnold 1983; Bijma and Wade 2008).

Previous models have treated inheritance and selection in isolation (Moore et al. 1997; Wolf et al. 1999). However, when traits function as interacting phenotypes, their effects on both stages of the evolutionary process are inexorably coupled. The same phenotypic interactions that affect the paths of inheritance within a population also are expected to affect the modes and targets of selection. We therefore seek to integrate previous work by deriving a general multivariate equation for the response to social and nonsocial selection. Our results demonstrate that a response to social selection is predicted whenever there is a nonzero covariance between breeding values in one individual and the phenotype of its social partner or the mean phenotype of its group. This critical covariance may arise from relatedness (or other similar associations between direct breeding values), IGEs, or both. Our results reveal a fundamental symmetry between coefficients of relatedness and the strength of IGEs. We provide examples showing how the symmetry between relatedness and IGEs alters the predictions of Hamilton's (1963, 1964a,b) rule for the evolution of altruism, and

how altruism, greenbeards, aggression, and weapons can evolve by social selection and IGEs.

Evolutionary Response to Social Selection

A GENERAL EQUATION

In the most general sense, interacting phenotypes are either traits that affect the phenotype or fitness of another individual or traits that are affected by interacting with another individual. Such traits tend to be subject to two types of selection. As with any trait, individual, or nonsocial, selection arises when the fitness of the focal individual is affected by its own phenotype. When the fitness of a focal individual is affected by the phenotype of a social partner or partners, social selection occurs (Wolf et al. 1999). The contribution of social selection to the total covariance between phenotype and fitness (the selection differential, s) depends on the covariance between the phenotypes of the focal individual and its social partner. In matrix notation,

$$\mathbf{s} = \mathbf{P}\boldsymbol{\beta}_\mathbf{N} + \mathbf{C}^\mathbf{I}\boldsymbol{\beta}_\mathbf{S}, \quad (1)$$

where $\mathbf{s}$ is a column vector of selection differentials, $\mathbf{P}$ represents the phenotypic variance–covariance matrix, $\mathbf{C}^\mathbf{I}$ is the matrix of covariances among the phenotypes of interactants, $\boldsymbol{\beta}_\mathbf{N}$ is a column vector of individual, or nonsocial, selection gradients, and $\boldsymbol{\beta}_\mathbf{S}$ is a column vector of social selection gradients (cf. equation 11 of Wolf et al. 1999). This approach to partitioning selection corresponds to the "neighbor" approach derived by Okasha (2006) from the results of Nunney (1985). (Throughout our derivation, we use matrix notation to achieve multivariate generality. The one-trait and two-trait examples discussed in earlier papers [Moore et al. 1997; Wolf et al. 1999] can be derived from the multivariate equations presented here). To facilitate following models, we provide in Table 1 a summary of the notation used in this article.

Equation (1) shows that a nonzero $\mathbf{C}^\mathbf{I}$ is necessary for social selection to contribute to overall phenotypic selection on a trait. However, the $\mathbf{s}$ vector in equation (1) cannot simply be substituted into the multivariate breeder's equation, $\Delta\bar{\mathbf{z}} = \mathbf{G}\mathbf{P}^{-1}\mathbf{s}$ (where $\mathbf{G}$ is the additive genetic (co)variance matrix, Lande 1979) to predict the evolutionary response to selection (represented by the vector of changes in mean trait values, $\Delta\bar{\mathbf{z}}$). This is because $\mathbf{C}^\mathbf{I}$ can reflect both heritable and environmental sources of covariance. For example, a nonzero $\mathbf{C}^\mathbf{I}$ may arise when the phenotypes of neighbors covary solely because they exist in more similar environments relative to some other group of neighbors; that is, there is environmentally determined population subdivision.

We next use Price's theorem (Robertson 1966; Li 1967; Price 1970) to derive generalized equations for the response to simultaneous social and nonsocial selection (see also Frank 1997, 1998; Rice 2004; Bijma et al. 2007a; Bijma and Wade 2008). We first develop the equations for pairs of interacting individuals for simplicity and later extend the case to larger groups. Price's theorem

Table 1. Notation used in this article.

Symbol	Meaning
$\mathbf{a}$, $\mathbf{e}$	Vectors of additive genetic and residual values
$\mathbf{a_S}$, $\mathbf{e_S}$	Vectors of social (indirect) breeding and residual values (Bijma et al. 2007a; McGlothlin and Brodie 2009)
$\mathbf{A}$	Vector of total breeding values (Moore et al. 1997; Bijma et al. 2007a; McGlothlin and Brodie 2009)
$\boldsymbol{\beta}_\mathbf{N}$	Vector of nonsocial ("natural") selection gradients (Wolf et al. 1999)
$\boldsymbol{\beta}_\mathbf{S}$	Vector of social selection gradients (Wolf et al. 1999)
$\mathbf{C_{Az}}$, $\mathbf{C_{Az'}}$	Covariance matrices of a focal individual's total breeding values with its own phenotypes and those of an interactant
$\mathbf{C}^\mathbf{I}$	Matrix of phentoypic covariance between interacting individuals (Wolf et al. 1999)
$\mathbf{G}$	Additive genetic variance–covariance matrix (Lande 1979)
$\mathbf{G_D}$	Variance–covariance matrix of direct breeding values (McGlothlin and Brodie 2009)
$\mathbf{G_{DS}}$, $\mathbf{G_{SD}}$	Covariance matrix of direct and social breeding values and its transpose (McGlothlin and Brodie 2009)
$\mathbf{G_S}$	Variance–covariance matrix of social breeding values (McGlothlin and Brodie 2009)
n	Group size
$\mathbf{P}$	Phenotypic variance–covariance matrix (Lande 1979)
$\boldsymbol{\Psi}$	Matrix of indirect genetic effects coefficients ψ_{ij} (Moore et al. 1997)
r, $\mathbf{R}$	Univariate and multivariate relatedness
$\mathbf{s}$	Multivariate selection differential, a vector (Lande 1979)
w	Relative fitness, a scalar
$\mathbf{z}$, $\mathbf{z'}$	Vectors of focal individual and interactant phenotypes (Moore et al. 1997)
$\Delta\bar{\mathbf{z}}$	Multivariate evolutionary change in phenotypic mean, a vector (Lande 1979)

states that the change in mean phenotype is equal to the covariance between total breeding values and fitness, or

$$\Delta\bar{\mathbf{z}} = \mathrm{cov}(\mathbf{A}, w), \tag{2}$$

where $\mathbf{A}$ is a vector of total breeding values for each phenotype of interest. An individual's total breeding value represents its expected contribution to average offspring phenotype, and may consist of both direct and indirect genetic effects (Falconer and MacKay 1996; Moore et al. 1997; Bijma et al. 2007a; McGlothlin and Brodie 2009). Following Wolf et al. (1999), we represent relative fitness, w, as a regression equation including the vectors of focal-individual and social-partner phenotypic values,

$$w = \alpha + \mathbf{z}^{\mathrm{T}}\boldsymbol{\beta}_{\mathbf{N}} + \mathbf{z}'^{\mathrm{T}}\boldsymbol{\beta}_{\mathbf{S}} + \varepsilon, \tag{3}$$

where α is an intercept, ε is an error term, $\mathbf{z}$ is a vector of phenotypic values in focal individuals, $\mathbf{z}'$ is a vector of phenotypes in social partners, and T denotes matrix transposition (Fig. 1). Throughout our derivation, we use a prime to denote variables that belong to a social partner rather than the focal individual.

Substituting equation (3) into equation (2), we find

$$\begin{aligned}\Delta\bar{\mathbf{z}} &= \mathrm{cov}\left(\mathbf{A}, \alpha + \mathbf{z}^{\mathrm{T}}\boldsymbol{\beta}_{\mathbf{N}} + \mathbf{z}'^{\mathrm{T}}\boldsymbol{\beta}_{\mathbf{S}} + \varepsilon\right)\\ &= \mathrm{cov}(\mathbf{A}, \mathbf{z}^{\mathrm{T}})\boldsymbol{\beta}_{\mathbf{N}} + \mathrm{cov}(\mathbf{A}, \mathbf{z}'^{\mathrm{T}})\boldsymbol{\beta}_{\mathbf{S}},\end{aligned} \tag{4a}$$

which can be written in a compact form as

$$\Delta\bar{\mathbf{z}} = \mathbf{C}_{\mathbf{Az}}\boldsymbol{\beta}_{\mathbf{N}} + \mathbf{C}_{\mathbf{Az'}}\boldsymbol{\beta}_{\mathbf{S}}. \tag{4b}$$

Equation (4b) shows that the portion of evolutionary change attributable to nonsocial selection is proportional to the matrix of covariances between the focal individuals' total breeding values and their own phenotypic values ($\mathbf{C}_{\mathbf{Az}}$). Similarly, the portion of evolutionary change due to social selection is proportional to the matrix of covariances between the focal individuals' breeding values and the phenotypic values of their social partners ($\mathbf{C}_{\mathbf{Az'}}$). In other words, in order for evolutionary change to occur, a nonrandom association between the genes of individuals and the phenotypes of their social partners must accompany social selection. The causes of a nonzero $\mathbf{C}_{\mathbf{Az'}}$ can be divided into two general classes: either individuals are associated nonrandomly based on their genotypes (e.g., relatedness) or phenotypic expression is influenced by the association between individuals (IGEs).

Below, we explore the components of the covariance matrices using a trait-based model of IGEs (Moore et al. 1997). In Appendix A, we illustrate the equivalence between the trait-based approach adopted here and the phenotypic variance component models of IGEs of Griffing (1967, 1969, 1976, 1981a) and Bijma and colleagues (Bijma et al. 2007a,b; Bijma and Wade 2008).

RELATEDNESS AND IGEs

The phenotypic vectors of two interacting individuals are defined as

$$\mathbf{z} = \mathbf{a} + \mathbf{e} + \boldsymbol{\Psi}\mathbf{z}' \tag{5a}$$

$$\mathbf{z}' = \mathbf{a}' + \mathbf{e} + \boldsymbol{\Psi}\mathbf{z}, \tag{5b}$$

where the strength and direction of IGEs is described by the square matrix of interaction coefficients $\boldsymbol{\Psi}$, which consists of elements ψ_{ij} describing the effect of trait j in an interactant on trait i in a focal individual (Moore et al. 1997). Again, throughout this derivation, we use primes to denote that a variable belongs to the focal individual's social partner.

Substituting equation (5b) into (5a) and vice versa, the phenotypic vectors can be defined explicitly as

$$\mathbf{z} = (\mathbf{I} - \boldsymbol{\Psi}\boldsymbol{\Psi})^{-1}(\mathbf{a} + \mathbf{e} + \boldsymbol{\Psi}\mathbf{a}' + \boldsymbol{\Psi}\mathbf{e}') \tag{6a}$$

$$\mathbf{z}' = (\mathbf{I} - \boldsymbol{\Psi}\boldsymbol{\Psi})^{-1}(\mathbf{a}' + \mathbf{e}' + \boldsymbol{\Psi}\mathbf{a} + \boldsymbol{\Psi}\mathbf{e}), \tag{6b}$$

where $\mathbf{a}$ is a column vector of additive genetic values, $\mathbf{e}$ is a column vector of environmental effects, $\mathbf{I}$ represents the identity matrix (Fig. 1). As in Moore et al. (1997), we assume that the total effects of interacting phenotypes can be decomposed into additive genetic ($\boldsymbol{\Psi}\mathbf{a}'$) and environmental effects ($\boldsymbol{\Psi}\mathbf{e}'$). That is, we assume the effects of a social partner's genes and environment on the expression of a focal individual's phenotypes occur solely via effects of the social partner's phenotype (Fig. 1). The factor $(\mathbf{I} - \boldsymbol{\Psi}\boldsymbol{\Psi})^{-1}$ represents the potential for feedback, which arises because traits in the two individuals may simultaneously affect one another (see Moore et al. 1997 for derivation). The vector of total breeding values can be determined by solving for an individual's additive genetic contribution to the expectation of equation (5a),

$$\mathbf{A} = (\mathbf{I} - \boldsymbol{\Psi}\boldsymbol{\Psi})^{-1}(\mathbf{a} + \boldsymbol{\Psi}\mathbf{a}),$$

and simplifying,

$$\mathbf{A} = (\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{a} \tag{7}$$

(see Moore et al. 1997 for derivation). Substituting equations (6) and (7) into equation (4a), we find

$$\begin{aligned}\Delta\bar{\mathbf{z}} = {} & \mathrm{cov}[(\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{a}, [(\mathbf{I} - \boldsymbol{\Psi}\boldsymbol{\Psi})^{-1}(\mathbf{a} + \mathbf{e} + \boldsymbol{\Psi}\mathbf{a}' + \boldsymbol{\Psi}\mathbf{e}')]^{\mathrm{T}}]\boldsymbol{\beta}_{\mathbf{N}}\\ & + \mathrm{cov}[(\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{a}, [(\mathbf{I} - \boldsymbol{\Psi}\boldsymbol{\Psi})^{-1}(\mathbf{a}' + \mathbf{e}' + \boldsymbol{\Psi}\mathbf{a} + \boldsymbol{\Psi}\mathbf{e})]^{\mathrm{T}}]\boldsymbol{\beta}_{\mathbf{S}}.\end{aligned} \tag{8}$$

To simplify this equation, we make the standard quantitative genetic assumption that all covariances between additive genetic values and residual (environmental) values are zero, giving

$$\Delta\bar{\mathbf{z}} = (\mathbf{I} - \boldsymbol{\Psi})^{-1}[\mathbf{G} + \mathrm{cov}(\mathbf{a}, \mathbf{a'}^{\mathrm{T}})\boldsymbol{\Psi}^{\mathrm{T}}](\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{N}} + (\mathbf{I} - \boldsymbol{\Psi})^{-1}[\mathrm{cov}(\mathbf{a}, \mathbf{a'}^{\mathrm{T}}) + \mathbf{G}\boldsymbol{\Psi}^{\mathrm{T}}](\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{S}}. \quad (9)$$

When $\mathrm{cov}(\mathbf{a}, \mathbf{a'}^{\mathrm{T}})$ arises because interacting individuals are related or due to population genetic structure, $\mathrm{cov}(\mathbf{a}, \mathbf{a'}^{\mathrm{T}}) = r\mathbf{G}$, where r is the coefficient of relatedness, and equation (9) simplifies to

$$\Delta\bar{\mathbf{z}} = (\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{G}(\mathbf{I} + r\boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{N}} + (\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{G}(r\mathbf{I} + \boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{S}}. \quad (10)$$

The formulation in equation (10) uses a regression-based definition of relatedness, which can incorporate both pedigree relatedness and population structure (Wright 1965; Hamilton 1972; Michod and Hamilton 1980; Uyenoyama and Feldman 1981; Uyenoyama 1984; Grafen 1985; Queller 1992b; Bijma et al. 2007a). Hamilton's regression definition was stated in its most general form, $r = \frac{\mathrm{cov}(a,\ a')}{\mathrm{var}(a)}$, by Queller (1992b). In most cases, r will be zero or positive, but may be negative if individuals avoid relatives as social partners more than would be expected at random (Hamilton 1972; Rousset 2002; Konovalov and Heg 2008).

Equation (10) assumes that relatedness is uniform across all traits. This assumption is likely to be violated whenever individuals assort nonrandomly based on specific phenotypes, as might occur in trait-group or greenbeard models (Hamilton 1964b; Wilson 1975; Dawkins 1976; Wilson and Dugatkin 1997; Wolf et al. 1999; Pepper 2000; Jansen and van Baalen 2006; Grafen 2009; Gardner and West 2010). To encompass such situations and achieve greater generality, we define a matrix of association among breeding values as

$$\mathbf{R} = \mathrm{cov}(\mathbf{a}, \mathbf{a'}^{\mathrm{T}})\mathbf{G}^{-1}, \quad (11)$$

which is a simple multivariate extension of Queller's (1992b) expression of additive genetic relatedness. $\mathbf{R}$ is a square matrix of partial regression coefficients r_{ij} that describe the translation between the additive genetic values of focal individuals and their interactants. In general, $\mathrm{cov}(\mathbf{a}, \mathbf{a'}^{\mathrm{T}})$ will tend to be symmetrical, but $\mathbf{R}$ will not. Incorporating $\mathbf{R}$ into equation (9) and simplifying, we find

$$\Delta\bar{\mathbf{z}} = (\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{G}(\mathbf{I} + \mathbf{R}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{N}} + (\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{G}(\mathbf{R}^{\mathrm{T}} + \boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{S}}. \quad (12)$$

When relatedness is uniform across traits, $\mathbf{R} = r\mathbf{I}$, and equation (12) reduces to equation (10). Otherwise, it is difficult to determine the structure of $\mathbf{R}$ based on a priori expectations, although specific structures may be postulated to explore specific models of social evolution. For example, in a true greenbeard situation, individuals assort nonrandomly based on a single recognizible trait that signals (z_i) the propensity to behave altruistically (Dawkins 1976; Gardner and West 2010). Here, $\mathbf{R}$ could be modeled as zero except for a single diagonal element r_{ii}. Off-diagonal elements of $\mathbf{R}$ would be nonzero when one trait in a focal individual predicts an association with a second trait in its partner, as in the coevolution of male ornaments and female preference in sexual selection (Lande 1981; Kirkpatrick 1982). $\mathbf{R}$ is therefore a parameter that can be experimentally measured to test predictions associated with specific models of social evolution.

Equation (12) is general and can be applied to many specific situations. In the absence of IGEs and social selection, equation (12) simplifies to the standard multivariate breeder's equation (Lande 1979; Lande and Arnold 1983). In the Discussion, we present worked examples for two traits showing how IGEs and social selection combine to lead to evolution of traits such as altruism, greenbeards, aggression, and weapons.

EVOLUTIONARY RESPONSES TO SOCIAL VERSUS NONSOCIAL SELECTION

To understand how the response to social selection differs from the response to nonsocial selection, we can examine equation (12) in detail. Comparing equations (12) and (4b), we see that the portion of the evolutionary response due to nonsocial selection is determined by $\mathbf{C_{Az}}$ and that this matrix can be defined as

$$\mathbf{C_{Az}} = (\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{G}(\mathbf{I} + \mathbf{R}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}. \quad (13)$$

Similarly, the response to social selection is determined by $\mathbf{C_{Az'}}$, which is defined as

$$\mathbf{C_{Az'}} = (\mathbf{I} - \boldsymbol{\Psi})^{-1}\mathbf{G}(\mathbf{R}^{\mathrm{T}} + \boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}. \quad (14)$$

Common to both responses are the factors $(\mathbf{I} - \boldsymbol{\Psi})^{-1}$ and $(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}$, which represent the linear and feedback influences, respectively, of IGEs on phenotypic expression (Moore et al. 1997; Bleakley et al. 2010). Thus, the portions of evolutionary change due to nonsocial and social selection are influenced equally by two of the main effects of IGEs: alteration of the relationship between genotype and phenotype and the acceleratory effects of feedback between interacting individuals.

The unique effects of relatedness (or other nonrandom assortment of breeding values) and IGEs are encompassed in the factors $(\mathbf{I} + \mathbf{R}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})$ and $(\mathbf{R}^{\mathrm{T}} + \boldsymbol{\Psi}^{\mathrm{T}})$ (and, when relatedness is assumed to be uniform across traits, their analogs in eq. 10). The first factor represents an interaction between relatedness and IGEs and shows that the response to nonsocial selection is generally increased by IGEs that occur among related individuals (Griffing 1976, 1981b; Bijma et al. 2007a; Ellen et al. 2007; Bijma and Wade 2008). The second factor shows that both relatedness and IGEs contribute to the response to social selection (Griffing 1976; Muir 1996; Bijma et al. 2007a; Bijma and Wade 2008), and do so independently and symmetrically.

EFFECTS OF GROUP SIZE

Although our treatment so far has been limited to interactions between two individuals to illustrate basic concepts, social interactions often involve multiple individuals. With multiple social partners, fitness can be expressed as

$$w = \alpha + \mathbf{z}^{\mathrm{T}}\boldsymbol{\beta}_{\mathbf{N}} + (n-1)\bar{\mathbf{z}}'^{\mathrm{T}}\boldsymbol{\beta}_{\mathbf{S}} + \varepsilon, \tag{15}$$

where the social selection gradient is defined as a single interactant's contribution to the fitness of a focal individual and n represents group size. The mean phenotype of a focal individual's social partners is represented by $\bar{\mathbf{z}}'$. Equation (15) assumes that groups are of equal size, but may be extended to include variable group sizes by replacing n with the arithmetic mean group size, $\bar{n}$. When group-level selection is of interest, fitness can be defined equivalently as

$$w = \alpha + \mathbf{z}^{\mathrm{T}}\boldsymbol{\beta}_{\mathbf{N}} + \bar{\mathbf{z}}'^{\mathrm{T}}\boldsymbol{\beta}_{group} + \varepsilon, \tag{16}$$

which makes no assumption about group size. We may use Price's equation (2) to predict the evolution of the global mean phenotype ($\Delta\bar{\bar{\mathbf{z}}}$) by substituting equation (15), obtaining

$$\Delta\bar{\bar{\mathbf{z}}} = \mathrm{cov}(\mathbf{A}, \mathbf{z}^{\mathrm{T}})\boldsymbol{\beta}_{\mathbf{N}} + (n-1)\mathrm{cov}(\mathbf{A}, \bar{\mathbf{z}}'^{\mathrm{T}})\boldsymbol{\beta}_{\mathbf{S}}. \tag{17}$$

Equation (17) assumes that group size is either invariant, or (replacing n with $\bar{n}$) is variable but has no genetic basis, but otherwise, equation (17) is general and applicable to populations with any group structure. To quantify the influences of relatedness versus IGEs, the group structure must be specified explicitly. In Appendix B, we derive the case for a population with equally sized, nonoverlapping groups of n individuals, which yields

$$\begin{aligned}\Delta\bar{\bar{\mathbf{z}}} = {} & [\mathbf{I} - (n-1)\boldsymbol{\Psi}]^{-1}\mathbf{G}[\mathbf{I} - (n-2)\boldsymbol{\Psi}^{\mathrm{T}} + r(n-1)\boldsymbol{\Psi}^{\mathrm{T}}] \\ & \times [\mathbf{I} - (n-2)\boldsymbol{\Psi}^{\mathrm{T}} - (n-1)\boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}}]^{-1}\boldsymbol{\beta}_{\mathbf{N}} \\ & + (n-1)[\mathbf{I} - (n-1)\boldsymbol{\Psi}]^{-1}\mathbf{G}(r\mathbf{I} + \boldsymbol{\Psi}^{\mathrm{T}}) \\ & \times [\mathbf{I} - (n-2)\boldsymbol{\Psi}^{\mathrm{T}} - (n-1)\boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}}]^{-1}\boldsymbol{\beta}_{\mathbf{S}}. \end{aligned} \tag{18}$$

We also derive an equivalent equation using the variance-components framework in Appendix B.

Examination of equation (18) reveals that group size affects both the linear and feedback effects of $\boldsymbol{\Psi}$ for both nonsocial and social selection. The effect of group size on the response to selection when IGEs are present will depend on the direction and magnitude of the elements of $\boldsymbol{\Psi}$. The single-trait case is particularly instructive, as an IGE between the same trait in two interactants can cause a strong feedback effect that drastically increases the response to selection (see Moore et al. 1997, Fig. 3B). Figure 2 shows the change in the evolutionary response to nonsocial selection and social selection when group size and IGEs are considered relative to a model that includes only direct genetic effects. Using

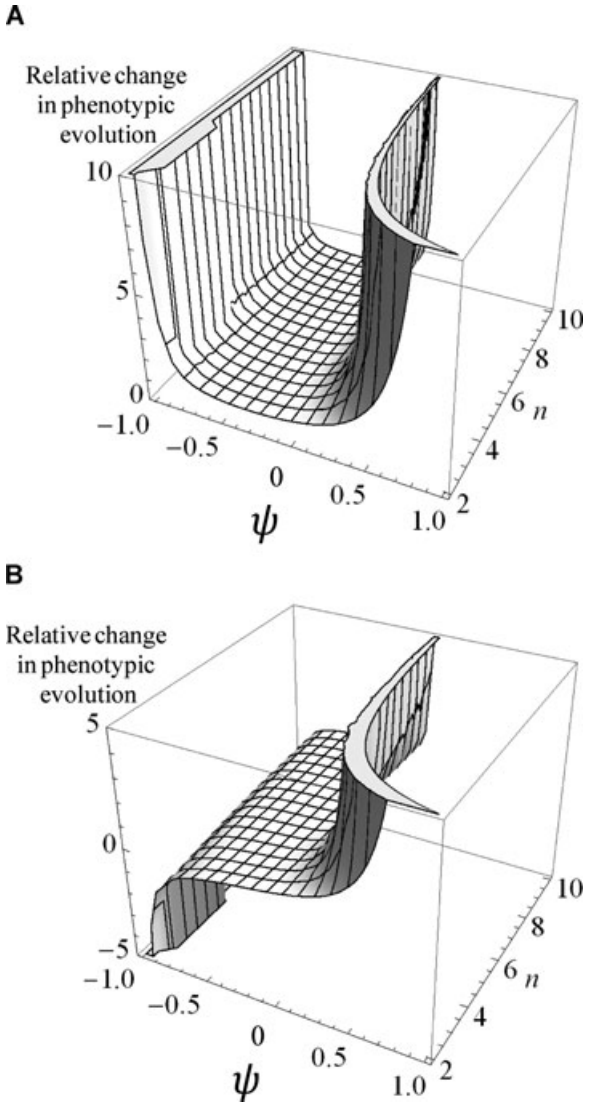

Figure 2. Relative change in the portion of evolutionary response of a single trait due to (A) nonsocial and (B) social selection as a function of the strength of the indirect genetic effect (ψ) and group size (n), when compared to a model that does not include indirect genetic effects (see equations 19 and 20 to derive A and B, respectively). Note that in both graphs, the range of is limited to $-1 < \psi < 1/(n-1)$.

a single-trait version of equation (18) with $r = 0$, these can be shown to be

$$\frac{1-(n-2)\psi}{[1-(n-1)\psi][1-(n-2)\psi-(n-1)\psi^2]} \tag{19}$$

for the response to nonsocial selection and

$$\frac{(n-1)\psi}{[1-(n-1)\psi][1-(n-2)\psi-(n-1)\psi^2]} \tag{20}$$

for the response to social selection. The result is that for $\psi > 0$, the evolutionary rate rapidly approaches infinity as ψ increases, but does so for smaller values of ψ as group size increases. However,

when $\psi < 0$, group size has very little effect. In other words, it takes a very large negative ψ to create evolutionary acceleration regardless of group size, but a very small positive ψ can have very large effects if the group size is large. The ratios in equations (19) and (20) suggest that for a single-trait system, $-1 < \psi < 1/(n-1)$, because at the boundaries of this range, the denominator equals zero. Ultimately, determining the sign and magnitude of ψ is an empirical question and provides a test of our model's predictions regarding social evolution.

The pattern of response to selection in Figure 2 arises primarily because as groups become larger, positive values of ψ decrease the denominator in equations (19) and (20) more quickly than do negative values of ψ. This occurs due to two separate effects. First, the linear effect of IGEs, $[1-(n-1)\psi]^{-1}$, decreases when $\psi < 0$ but increases when $\psi > 0$. This effect compensates for the effect of group size on the numerator in equation (19), which decreases with $(n-2)$. Second, the feedback effect of IGEs, $[1-(n-2)\psi-(n-1)\psi^2]^{-1}$, increases with increasing group size when $\psi > 0$ but decreases with increasing group size when $\psi < 0$. This is caused by the term $(n-2)\psi$.

These considerations suggest that positive feedback is more effective at producing evolutionary acceleration than is negative feedback. This asymmetry may be visualized by thinking of positive values of ψ as attractive forces that act to make pairs of interacting individuals more similar. With positive values of ψ, even small effects can act to make all individuals in a group nearly identical. Negative values of ψ may be visualized as repellent forces, pushing phenotypes of pairs of individuals in a group away from each other. As groups become larger, any given pair of phenotypes cannot be spread apart maximally because these phenotypes are simultaneously affected by the phenotypes of all the other group members.

The results above decompose IGEs caused by group interactions into cumulative effects of individuals. However, in certain systems, particularly when groups are large, it may be simpler to consider total effects of a group on phenotypic expression. Such group-level IGEs can be encompassed in the matrix $\boldsymbol{\Psi}_{group}$ (McGlothlin and Brodie 2009).

Altruism, Social Selection, and IGEs

HAMILTON'S RULE EXTENDED

We analyze the evolution of altruism using our model to illustrate the similar but independent roles of relatedness and IGEs in determining the response to social selection. As summarized by Hamilton's rule, altruism should increase in frequency if the cost to the performer (C) is outweighed by the benefit to the recipient (B) multiplied by the relatedness of the two individuals (r) (Hamilton 1963, 1964a, b). Symbolically, altruism increases when

$$C < rB. \tag{21}$$

In the notation of phenotypic selection, $-\beta_N$ and β_S naturally correspond to C and B in Hamilton's formulation, because they measure the fitness cost of possessing a given trait value z and the fitness benefit of interacting with an individual possessing trait value z' (Wolf et al. 1999). This notation emphasizes that the problem of altruism arises when two levels of selection—nonsocial and social—act in opposition to each other (Price 1972; Hamilton 1975; Wade 1985; Taylor and Frank 1996; Wilson and Wilson 2007).

Wolf et al. (1999; Wolf and Moore 2010) derive a phenotypic version of Hamilton's rule based on equation (1), which can be used as a heuristic tool when genetic data are unavailable. Similarly, Goodnight et al. (1992; Goodnight 2005) derives Hamilton's rule in terms of individual- and group-level selection. However, the phenotypic versions of Hamilton's rule cannot be used to quantitatively predict the evolution of altruistic traits, because they consider only selection and not the inheritance that mediates the response across generations. Here, we derive a general version of Hamilton's rule for interacting phenotypes. For simplicity, we consider only a single-trait case for a pair of interacting individuals, but our derivation can be easily extended to describe multivariate suites of traits or larger groups. Using a univariate version of equation (4b) and asking when the phenotype z will increase (i.e., when $\Delta\bar{z} > 0$):

$$0 < C_{Az}\beta_N + C_{Az'}\beta_S, \tag{22a}$$

which can be simplified to

$$-\beta_N < \frac{C_{Az'}}{C_{Az}}\beta_S. \tag{22b}$$

This inequality is identical to the general version of Hamilton's rule derived by Queller (1985, 1992b). The ratio $\frac{C_{Az'}}{C_{Az}}$ is a measure of the similarity of interacting individuals. It will tend to be proportional to the phenotypic correlation between interactants (the defining parameter of the phenotypic Hamilton's rule; Wolf et al. 1999), but measures only genetic effects.

In a one-trait model with relatedness and IGEs, C_{Az} and $C_{Az'}$ are defined as

$$C_{Az} = G\frac{1+r\psi}{(1-\psi)(1-\psi^2)} \tag{23}$$

and

$$C_{Az'} = G\frac{r+\psi}{(1-\psi)(1-\psi^2)}. \tag{24}$$

Substituting these definitions into inequality (22b), we find

$$-\beta_N < \frac{r+\psi}{1+r\psi}\beta_S. \tag{25}$$

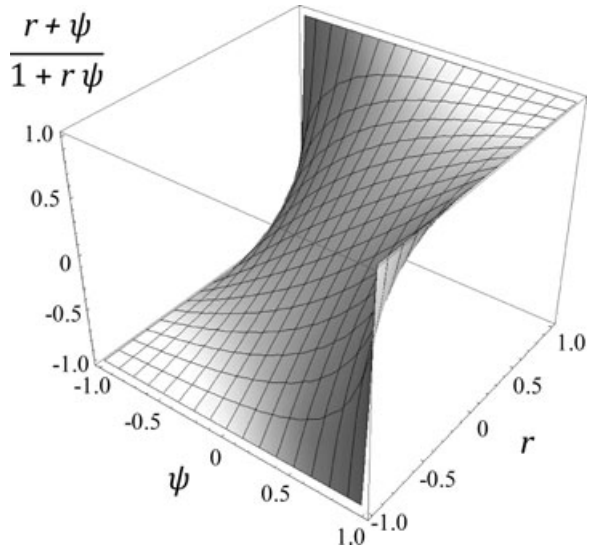

Figure 3. Contribution of the indirect genetic effect (ψ) and relatedness (r) to the evolution of a single altruistic trait (inequality 25). The balance between social and nonsocial selection in the extended version of Hamilton's rule is determined by the quantity plotted on the vertical axis. See text for discussion.

This formulation shows that r and ψ have symmetrical effects on the evolution of altruism (Fig. 3). Indeed, when there are no IGEs, $\psi = 0$ and our result reduces to the typical formulation of Hamilton's rule (albeit expressed with different notation):

$$-\beta_N < r\beta_S. \tag{26}$$

Similarly, when $r = 0$,

$$-\beta_N < \psi\beta_S. \tag{27}$$

This result shows the similarity of r and ψ. Both r and ψ can be expressed as regression coefficients: r is the regression of an individual's direct genetic effect on its partner's direct genetic effect (Hamilton 1972), whereas ψ is the regression of an individual's direct genetic effect on its partner's indirect genetic effect (McGlothlin and Brodie 2009). In this sense, ψ can be thought of as a measure of indirect genetic relatedness. Both of these components of relatedness are encompassed by Queller's (1985, 1992b) generalized definition of relatedness, which in our notation is expressed as $\frac{C_{Az'}}{C_{Az}}$. The advantage of distinguishing direct genetic relatedness from indirect genetic relatedness is the potential to parse evolutionary consequences of interactions among relatives from those due to phenotypic influences that may occur between unrelated individuals.

Inequality (27) demonstrates that altruism should be able to evolve without direct genetic relatedness, as long as IGEs provide indirect genetic relatedness (see also Bijma and Wade 2008). This is consistent with the view that all models of altruism require some form of relatedness (West et al. 2007, 2008) but helps explain some of the controversy as the genetic effects need not be direct. For the single-trait case, ψ must be positive in order for IGEs to drive the evolution of altruism. When $\psi > 0$, the phenotypes of two interacting individuals become more similar (Moore et al. 1997). Thus, ψ may be considered to represent the strength of reciprocity (Bleakley and Brodie 2009; Bleakley et al. 2010), and to the extent that altruism depends upon ψ, it may be considered reciprocal altruism (Trivers 1971; Axelrod and Hamilton 1981). In addition to reciprocity, ψ may be used to model other behavioral mechanisms such as manipualtion or punishment, that may lead to cooperation between individuals (Clutton-Brock 2009).

INCLUSIVE FITNESS

In addition to deriving a general rule for the evolution of altruism, Hamilton (1964a) defined the concept of inclusive fitness, a measure of fitness that takes into account how one's actions affect one's relatives. According to Hamilton, an individual's inclusive fitness can be defined as personal fitness when social effects of neighbors are removed but social effects on neighbors, weighted by relatedness, are added. Hamilton (1964a) and others (Grafen 2006, 2007; Gardner and Grafen 2009; Bijma 2010) have argued that selection tends to maximize or optimize inclusive fitness. However, measuring inclusive fitness is not always straightforward, particularly for phenotypes (Grafen 1982; Creel 1990; Lucas et al. 1996; Queller 1996). It has even been suggested that inclusive fitness may differ across traits, making the notion of measuring an individual's inclusive fitness impossible (Queller 1996).

Using our model, it can be shown that inclusive fitness can be defined as a quantity belonging to an individual, even when multiple traits are considered. Expressing Hamilton's definition in our multivariate notation, we can define relative inclusive fitness as

$$w_{inc} = w - \mathbf{z'}^{\mathrm{T}}\boldsymbol{\beta}_{\mathbf{S}} + \mathbf{z}^{\mathrm{T}}\mathbf{C}_{\mathbf{Az}}^{-1}\mathbf{C}_{\mathbf{Az'}}\boldsymbol{\beta}_{\mathbf{S}} \tag{28}$$

This definition holds when individuals interact in pairs. For larger groups, the last two terms on the right-hand side should be weighted by group size. Substituting our definition of relative fitness (eq. 3), we see that

$$w_{inc} = \alpha + \mathbf{z}^{\mathrm{T}}\left(\boldsymbol{\beta}_{\mathbf{N}} + \mathbf{C}_{\mathbf{Az}}^{-1}\mathbf{C}_{\mathbf{Az'}}\boldsymbol{\beta}_{\mathbf{S}}\right) + \varepsilon. \tag{29}$$

Thus, an individual's inclusive fitness depends upon its own traits, nonsocial, and social selection acting on those traits, and the multivariate similarity between interacting pairs described by $\mathbf{C}_{\mathbf{Az}}^{-1}\mathbf{C}_{\mathbf{Az'}}$. This definition of inclusive fitness assumes that all pertinent traits (i.e., all interacting phenotypes) have been measured. It is easy to check that evolutionary change is reliably predicted using either relative fitness or relative inclusive fitness, or

$$\Delta\bar{\mathbf{z}} = \mathrm{cov}(\mathbf{A}, w) = \mathrm{cov}(\mathbf{A}, w_{inc}). \quad (30)$$

We can explore how relatedness and IGEs affect relative inclusive fitness by substituting equations (13–14) into equation (29) and simplifying,

$$w_{inc} = \alpha + \mathbf{z}^{\mathrm{T}}\big[\boldsymbol{\beta}_{\mathbf{N}} + (\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} + \mathbf{R}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1} \times (\mathbf{R}^{\mathrm{T}} + \boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{S}}\big] + \varepsilon. \quad (31)$$

Thus, if we are interested in estimating inclusive fitness, we must consider both relatedness and IGEs in addition to nonsocial and social selection. When relatedness is uniform across traits, this simplifies to

$$w_{inc} = \alpha + \mathbf{z}^{\mathrm{T}}\big[\boldsymbol{\beta}_{\mathbf{N}} + (\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} + r\boldsymbol{\Psi}^{\mathrm{T}})^{-1} \times (r\mathbf{I} + \boldsymbol{\Psi}^{\mathrm{T}})(\mathbf{I} - \boldsymbol{\Psi}^{\mathrm{T}}\boldsymbol{\Psi}^{\mathrm{T}})^{-1}\boldsymbol{\beta}_{\mathbf{S}}\big] + \varepsilon. \quad (32)$$

In the absence of IGEs this simplifies to

$$w_{inc} = \alpha + \mathbf{z}^{\mathrm{T}}(\boldsymbol{\beta}_{\mathbf{N}} + r\boldsymbol{\beta}_{\mathbf{S}}) + \varepsilon. \quad (33)$$

This multivariate formulation reveals that, even in the absence of IGEs, social selection is central to the estimation of Hamilton's original conception of inclusive fitness.

Discussion

The integration of selection and inheritance into a complete description of evolutionary change is usually simple and direct, as epitomized by the well-known breeder's equation (Lande 1979; Falconer and MacKay 1996). Social interactions substantially complicate this picture by generating covariances between genotypes of individuals and the phenotypes and fitness of their interactants. The results of our model demonstrate that to predict the evolution of interacting phenotypes we must know (1) how the genotypes of interacting individuals are related (whether through pedigree relatedness, population subdivision, or trait-specific associations), (2) how the phenotypes of interacting individuals affect one another's expression, and (3) how the phenotypes of interacting individuals socially affect fitness. These factors are above and beyond the additive genetic (co)variance and the strength of nonsocial selection, which must be measured to predict the evolution of any trait, social or otherwise (Lande 1979; Lande and Arnold 1983; Roff 1997; Kingsolver et al. 2001).

The equations presented here emphasize that social selection generates evolutionary change through a genetic pathway distinct from that responding to nonsocial selection (eq. 4b). Evolutionary response to social selection results only when the breeding value of a focal individual covaries with the phenotype of a social partner or social group. This is consistent with Queller's (1992b) general formulation of kin selection; however, our results demonstrate that the critical covariance might emerge via two biologically disparate paths—through relatedness or through phenotypic modification arising from IGEs. Although relatedness in this context is most likely to result from pedigree relationships or population subdivision, it is also conceivable that it reflects trait-specific associations among individuals. To encompass this multivariate possibility, we introduced the potentially asymmetric matrix $\mathbf{R}$ that describes trait-specific relatedness. This matrix allows situations in which organisms form groups based on specific attributes, such as in trait-group, greenbeard, and mate choice models to be incorporated into a multivariate predictive equation (Hamilton 1964b; Wilson 1975; Dawkins 1976; Lande 1981; Wilson and Dugatkin 1997; Pepper 2000; Grafen 2009; Gardner and West 2010).

Relatedness and IGEs have both independent and interactive effects on the response to selection. Both social and nonsocial selection is influenced by interacting phenotypes through the $\boldsymbol{\Psi}$ terms that account for linear and feedback influences on phenotypes (eqs. 10 and 12). These feedback effects are particularly exacerbated by group size and lead to dramatic increases in the rate of evolutionary response (Fig. 2). IGEs provide an additional contribution to the response to nonsocial selection when they occur among related individuals. Nevertheless, IGEs and relatedness have surprisingly independent and parallel contributions to the response to social selection. Our derivation of an extended Hamilton's rule emphasizes this symmetry, and suggests that relatedness and reciprocity should have nearly equal influences on the evolution of altruism (cf. Fletcher and Zwick 2006). Furthermore, because IGEs generate a covariance between interacting individuals via a genetic path, $\boldsymbol{\Psi}$ may be interpreted as a measure of indirect genetic relatedness. This result generalizes previous results that show how maternal effects should alter the predictions of Hamilton's rule to interactions occurring within a generation (Cheverud 1984; see Wolf 2003 for a similar treatment of this problem using variance components).

It is essential to recognize that although both phenomena originate through interactions among conspecifics, IGEs and social selection represent distinct mechanisms by which interacting phenotypes influence evolutionary change. These effects occur via different pathways (Fig. 1): social selection represents a direct relationship between the phenotype of social interactants and fitness, whereas IGEs influence fitness indirectly by influencing phenotypic expression. Both processes can create feedback that accelerates the rate of evolution, but on different time scales. IGEs create feedback by affecting phenotypic expression within a generation, thereby inflating the response to selection (Moore et al. 1997). Social selection creates feedback across generations because interacting phenotypes act simultaneously as targets and agents of selection. As the traits that cause social selection evolve, the next generation experiences a different social environment than the previous one. This social environment provides the basis

for selection, creating feedback in the evolution of the interacting phenotype (West-Eberhard 1979; Lande 1981; West-Eberhard 1983; Moore et al. 1997; Wolf et al. 1999).

This concept of social selection (Wolf et al. 1999) can be considered as a subset of the broader contextual models of multilevel selection (Goodnight et al. 1992; Queller 1992a; Bijma et al. 2007a; Bijma and Wade 2008). Hamilton's (1963, 1964a,b) inclusive fitness models have often been thought of as an alternative to multilevel selection as an explanation for the evolution of social behavior. Hamilton (1975) recognized that inclusive fitness models may be expressed as multilevel selection models, and subsequent analyses have demonstrated the mathematical equivalence between the two frameworks (Wade 1980; Queller 1992a; Bijma and Wade 2008). As demonstrated by our treatment of Hamilton's rule, considering IGEs and social selection provides additional insights into the inclusive-fitness framework. In addition, our model is composed of parameters that can be measured empirically to test hypotheses about social evolution.

EMPIRICAL APPLICATIONS

Of the components identified here as critical to understanding evolutionary response to social selection, substantial empirical progress has been made only for relatedness or population substructure. There are a number of well-established methods for measuring relatedness (Queller and Goodnight 1989; Ritland 1996; Lynch and Ritland 1999; Van de Casteele et al. 2001; Weir and Hill 2002; Csilléry et al. 2006; Weir et al. 2006; Konovalov and Heg 2008), and a wealth of data exists regarding relatedness and genetic structure in natural populations (Strassmann et al. 1989; Hughes 1998; Merilä and Crnokrak 2001; Cole 2003; Lukas et al. 2005; Leinonen et al. 2008).

There has been limited empirical investigation of IGEs, particularly nonmaternal IGEs (McGlothlin and Brodie 2009; Bleakley et al. 2010). Several recent studies have quantified IGEs as components of variance (e.g., Wolf 2003; Muir 2005; Petfield et al. 2005; Linksvayer 2006; Bergsma et al. 2008; Brommer and Rattiste 2008; Ellen et al. 2008; Danielson-Francois et al. 2009; Wilson et al. 2009), as changes in gene expression (Wang et al. 2008), as response to different genotypes (Linksvayer 2007; Kent et al. 2008; Linksvayer et al. 2009), or indirectly from selection lines (Moore et al. 2002; Chenoweth et al. 2010). Very few have examined IGEs within the multivariate trait-based framework that is necessary to identify the paths of influence between specific traits in interacting partners (Mutic and Wolf 2007; Bleakley and Brodie 2009; Galloway et al. 2009). New methodology for estimating $\boldsymbol{\Psi}$ (or its analog for maternal effects, $\mathbf{M}$; Kirkpatrick and Lande 1989) through components of quantitative genetic variance may address this paucity of data in the future (Galloway et al. 2009; McGlothlin and Brodie 2009).

Social selection gradients can be measured in a straightforward way using multiple regression techniques similar to contextual analysis (Heisler and Damuth 1987; Goodnight et al. 1992; Okasha 2006). As a purely phenotypic process, estimation of social selection does not require knowledge of the covariance of breeding values among interactants or other genetic information. Simultaneous social and nonsocial selection can be measured using a simple extension of Lande and Arnold's (1983) multiple regression method to include the traits of social interactants or groups in addition to those of the focal individual (Wolf et al. 1999). Depending on the population structure, investigators could perform such analyses using equations (3), (15), or (16) as regression models. Such an analysis differs subtly from traditional contextual analysis, which tends to use the group mean (including the focal individual) rather than the mean of the social interactants to estimate selection gradients (Okasha 2006). A few studies have used contextual analysis in plants (Stevens et al. 1995; Aspi et al. 2003; Donohue 2003, 2004; Weinig et al. 2007) and animals (Tsuji 1995; Banschbach and Herbers 1996; McAdam and Boutin 2003) but none have adopted the social selection approach we describe here.

In addition to the relatively large sample sizes and reliable estimates of individual fitness that are required for any study of selection in a natural population, the measurement of social selection requires information on the phenotypes of social partners or groups. However, large long-term selection datasets are becoming increasingly common in evolutionary biology (Kruuk et al. 2001, 2002; Grant and Grant 2002). It is likely that many existing datasets also contain information on social grouping that could be used to measure social selection. We encourage empiricists studying interacting phenotypes in natural populations to quantify nonsocial and social selection so that the importance of each may be determined.

ALTRUISM AND GREENBEARDS

To illustrate the applications of this theory, we present specific worked examples derived from the multivariate equation presented in the text (eq. 12). We focus on situations in which nonsocial and social selection are in conflict, that is, where a trait is beneficial to one individual in a pair but harmful to the other. We present examples involving two traits to emphasize how IGEs and social selection can lead to the coordinated evolution of interacting phenotypes.

First, suppose an altruistic behavior, z_1, benefits a recipient at the expense of the actor, so that it is under negative nonsocial selection ($\beta_{N1} < 0$) and positive social selection ($\beta_{S1} > 0$). A second trait, z_2, is a visible morphological trait, such as a badge, with no direct fitness consequences of its own ($\beta_{N2} = \beta_{S2} = 0$). However, individuals base their level of altruistic behavior on the morphological trait of their partner based on the coefficient ψ_{12}.

This morphological badge is determined by direct genetic and environmental effects, and is static within an individual.

We first assume that these two traits are genetically uncorrelated ($G_{12} = 0$) and that individuals assort at random ($\mathbf{R} = \mathbf{0}$). Using equation (12), the predicted evolutionary change in the two traits can be expressed as

$$\Delta\bar{z}_1 = G_{11}\beta_{N1} + {\psi_{12}}^2 G_{22}\beta_{S1} \tag{34a}$$

and

$$\Delta\bar{z}_2 = \psi_{12}G_{22}\beta_{S1}. \tag{34b}$$

The most obvious result is that the two traits are evolutionarily coupled, even in the absence of direct genetic covariance. This occurs via an interaction between the IGE of the cue on the altruistic behavior and the social selection gradient of the behavior. The evolution of altruism is not influenced by the sign of the IGE, and will evolve whenever

$$-\beta_{N1} < \frac{{\psi_{12}}^2 G_{22}}{G_{11}}\beta_{S1}. \tag{35}$$

For altruism to evolve, ψ_{12}, will have to be quite strong unless the relative cost of performing the behavior (β_{N1}) is quite low. In contrast, the evolution of the badge is determined by the sign of the IGE. The badge that elicits altruism will increase when

$$0 < \psi_{12}G_{22}\beta_{S1}. \tag{36}$$

Here, the combination of social selection and an IGE provides evolutionary feedback across generations. If the effect of the badge on the elicitation of altruistic behavior is positive ($\psi_{12} > 0$), then the two traits will tend to runaway together. However, if the badge's effect is negative ($\psi_{12} < 0$), the badge will evolve in the direction opposite of the behavior it elicits.

Another result of the inequalities above is that the badge will tend to evolve more quickly than the altruistic behavior it elicits. This occurs because the cue is not subject to nonsocial selection and because of the squared IGE coefficient in equation (34a).

We now allow individuals to assort nonrandomly based on the morphological trait. This is similar to a greenbeard model (Hamilton 1964b; Dawkins 1976; Gardner and West 2010), except that we assume no genetic correlation between the behavior and the badge. If individuals assort nonrandomly based solely on the morphological trait, the matrix $\mathbf{R}$ is no longer zero. Rather, it contains a single nonzero element, $r_{22'}$, that measures the strength of the relationship between the breeding values of the badge of the two interacting individuals. The evolution of the badge and altruism is now predicted by

$$\Delta\bar{z}_1 = \left(G_{11} + r_{22'}{\psi_{12}}^2 G_{22}\right)\beta_{N1} + {\psi_{12}}^2 G_{22}\beta_{S1} \tag{37a}$$

and

$$\Delta\bar{z}_2 = r_{22'}\psi_{12}G_{22}\beta_{N1} + \psi_{12}G_{22}\beta_{S1}. \tag{37b}$$

Nonrandom assortment adds an effect of nonsocial selection on the behavior to the evolution of the badge. Altruism now increases when

$$-\beta_{N1} < \frac{{\psi_{12}}^2 G_{22}}{G_{11} + r_{22'}{\psi_{12}}^2 G_{22}}\beta_{S1}, \tag{38}$$

and the badge increases when

$$-\beta_{N1} < \frac{1}{r_{22'}}\beta_{S1}. \tag{39}$$

The evolution of the badge is no longer dependent on IGEs, but instead depends upon the strength of assortment. Because this effect appears in the denominator, strong positive assortment slows the evolution of the cue. Positive assortment also decreases the rate of evolution of altruism slightly. The evolution of badge-based altruism is unlikely without genetic covariance between the behavior and the badge.

When a genetic correlation exists between the behavior and the badge, the evolution of the two traits is predicted by

$$\begin{aligned}\Delta\bar{z}_1 = {} & \left(G_{11} + \psi_{12}G_{12} + r_{22'}\psi_{12}G_{12} + r_{22'}{\psi_{12}}^2 G_{22}\right)\beta_{N1} \\ & + \left(\psi_{12}G_{12} + {\psi_{12}}^2 G_{22}\right)\beta_{S1}\end{aligned} \tag{40}$$

and

$$\Delta\bar{z}_2 = (G_{12} + r_{22'}\psi_{12}G_{22})\beta_{N1} + \psi_{12}G_{22}\beta_{S1}. \tag{41}$$

The evolution of altruism is now predicted when

$$-\beta_{N1} < \frac{\psi_{12}G_{12} + {\psi_{12}}^2 G_{22}}{G_{11} + \psi_{12}G_{12} + r_{22'}\psi_{12}G_{12} + r_{22'}{\psi_{12}}^2 G_{22}}\beta_{S1}, \tag{42}$$

and the badge increases when

$$-\beta_{N1} < \frac{\psi_{12}G_{22}}{G_{12} + r_{22'}\psi_{12}G_{22}}\beta_{S1}. \tag{43}$$

Here, the evolution of both traits is dominated by the strength of the IGE (ψ_{12}). In practice, as the genetic covariance between traits becomes stronger, it will be difficult to distinguish a situation such as the one above from a true greenbeard, where altruism and the visible signal are associated with the same gene (Gardner and West 2010). In the case in which the two traits become indistinguishable, their evolution will be predicted by the extended Hamilton's rule (inequality 25).

AGRESSION AND WEAPONS

As a second example, consider a two-trait system in which z_1 is aggressive behavior. When individuals interact, their level of aggression depends in part on the behavior of their partner ($\psi_{11} \neq 0$). In fights, success is determined both by the aggression of the focal individual ($\beta_{N1} > 0$) and that of its partner ($\beta_{S1} < 0$).

Success is also influenced by a morphological weapon (z_2; $\beta_{N2} > 0$, $\beta_{S2} < 0$). We assume aggressive behavior is not adjusted based on the partner's weapon ($\psi_{12} = 0$). (See Moore et al. 1997 eq. 23 for a similar example in the absence of social selection.) When interactions occur at random ($\mathbf{R} = \mathbf{0}$), the evolution of the two traits is predicted by

$$\Delta\bar{z}_1 = \frac{G_{11}}{(1-\psi_{11})\left(1-\psi_{11}{}^2\right)}(\beta_{N1} + \psi_{11}\beta_{S1}) + \frac{G_{12}}{(1-\psi_{11})}\beta_{N2} \tag{44}$$

and

$$\Delta\bar{z}_2 = \frac{G_{12}}{1-\psi_{11}{}^2}(\beta_{N1} + \psi_{11}\beta_{S1}) + G_{22}\beta_{N2}. \tag{45}$$

As is the case in the absence of social selection, the feedback effect of IGE on aggression magnifies the correlated evolutionary response of the weapon (Moore et al. 1997). However, the IGE has an additional effect when social selection is present. Assuming $\beta_{S1} < 0$, a negative ψ_{11} tends to lead to the evolution of greater aggression via the social selection pathway, whereas a positive ψ_{11} tends to lead to the evolution of less aggression. Biologically, this means that a tendency to act submissively to aggressive individuals leads to lead to an evolutionary increase in mean aggression, whereas a tendency to escalate fights leads to an evolutionary decrease in aggression. The evolutionary trajectory of weapons, of course, will depend on the sign of the genetic covariance as well.

Again, nonrandom assortment complicates matters further. One biologically plausible scenario is that individuals choose fighting partners based on a linear response to the size of their weapons. This would lead to a correlation between breeding values for weaponry, $r_{22'}$, in which case the response to selection would be predicted by

$$\Delta\bar{z}_1 = \frac{G_{11}}{(1-\psi_{11})\left(1-\psi_{11}{}^2\right)}(\beta_{N1} + \psi_{11}\beta_{S1}) + \frac{G_{12}}{1-\psi_{11}}(\beta_{N2} + r_{22'}\beta_{S2}) \tag{46}$$

and

$$\Delta\bar{z}_2 = \frac{G_{12}}{1-\psi_{11}{}^2}(\beta_{N1} + \psi_{11}\beta_{S1}) + G_{22}(\beta_{N2} + r_{22'}\beta_{S2}). \tag{47}$$

This is identical to the previous case, except now social selection on weapon size contributes to evolutionary change. Its effect will depend upon whether individuals assort positively (partners have similar weapons) or negatively (partners have oppositely sized weapons).

CONCLUSION

The results presented here, together with related theoretical work on the genetic ramifications of social interactions (Griffing 1967, 1969, 1976, 1981a; Moore et al. 1997; Wolf et al. 1999; Bijma et al. 2007a; Bijma and Wade 2008), demonstrate the importance of IGEs and social selection in the evolution of social behavior and other interacting phenotypes. Behavior, in particular, has long been viewed as having a central role in evolution, and various authors have considered it as both a facilitator and an inhibitor of evolutionary change (Roe and Simpson 1958; Mayr 1963; Bateson 2004; Duckworth 2009). The interacting phenotype models provide a quantitative framework that demonstrates how this conjecture can be true. IGEs and social selection provide mechanisms by which behavior and other interacting phenotypes influence the rate and direction of their own evolution. Both mechanisms can greatly accelerate the rate of evolutionary change and, in some cases, reverse the direction of evolution from that predicted in their absence. Here, we have identified the critical parameters to measure, allowing empiricists to test the importance of interacting phenotypes in driving evolutionary change.

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Appendix A

EQUIVALENCE OF VARIANCE-COMPONENTS MODELS OF IGEs

The framework of Griffing (1967, 1969, 1976, 1981a) and Bijma and colleagues (Bijma et al. 2007a,b; Bijma and Wade 2008) expresses IGEs as components of phenotypic variance rather than using the trait-based framework followed above. These two frameworks have been shown to provide equivalent measurements of the strengths of IGEs (McGlothlin and Brodie 2009). Here, we derive a multivariate version of the equation for evolutionary response derived by Bijma and Wade (2008) and show its equivalence to the trait-based equation.

In the variance-components framework, the total breeding value is equal to the sum of the direct and social (i.e., indirect genetic) breeding values. Expressed multivariately,

$$\mathbf{A} = \mathbf{a_D} + \mathbf{a_S}, \tag{A1}$$

where $\mathbf{a_D}$ and $\mathbf{a_S}$ are column vectors of direct and social breeding values, respectively. The former is proportional but not equal to the additive genetic value when IGEs display feedback (McGlothlin and Brodie 2009). The latter can be thought of as a genetic value for "social performance," encompassing the social effects of all of an individual's traits. The phenotypic vectors of two interacting individuals can be expressed as

$$\mathbf{z} = \mathbf{a_D} + \mathbf{e_D} + \mathbf{a'_S} + \mathbf{e'_S} \tag{A2a}$$

$$\mathbf{z'} = \mathbf{a'_D} + \mathbf{e'_D} + \mathbf{a_S} + \mathbf{e_S}, \tag{A2b}$$

where $\mathbf{e_D}$ and $\mathbf{e_S}$ terms are environmental (or residual effects). As above, primes designate effects belonging to a social partner of an individual. Note that the focal individual is affected by the social breeding value and environmental effect of its social partner, and vice versa.

Substituting these definitions into equation (4a), and making the standard quantitative genetic assumption of zero covariance between breeding values and residuals, we find

$$\begin{aligned}\Delta\bar{\mathbf{z}} = {} & \mathrm{cov}\left[(\mathbf{a_D} + \mathbf{a_S}), \left(\mathbf{a_D^T} + \mathbf{e_D^T} + \mathbf{a'^T_S} + \mathbf{e'^T_S}\right)\right]\boldsymbol{\beta_N} \\ & + \mathrm{cov}\left[(\mathbf{a_D} + \mathbf{a_S}), \left(\mathbf{a'^T_D} + \mathbf{e'^T_D} + \mathbf{a_S^T} + \mathbf{e_S^T}\right)\right]\boldsymbol{\beta_S}\end{aligned} \tag{A3a}$$

or in compact form,

$$\begin{aligned}\Delta\bar{\mathbf{z}} = {} & (\mathbf{G_D} + \mathbf{G_{DS'}} + \mathbf{G_{SD}} + \mathbf{G_{SS'}})\boldsymbol{\beta_N} \\ & + (\mathbf{G_{DD'}} + \mathbf{G_{DS}} + \mathbf{G_{SD'}} + \mathbf{G_S})\boldsymbol{\beta_S},\end{aligned} \tag{A3b}$$

where terms designated by $\mathbf{G}$ represent (co)variance matrices between breeding direct and/or social values and primes distinguish breeding values of the social partner from those of the focal individual (McGlothlin and Brodie 2009). Equation (17) is an analog of the trait-based equation (9). When interactants are related uniformly across traits, relatedness can be treated as a scalar, and equation (17) simplifies to

$$\Delta\bar{\mathbf{z}} = (\mathbf{G_D} + r\mathbf{G_{DS}} + \mathbf{G_{SD}} + r\mathbf{G_S})\boldsymbol{\beta_N} + (r\mathbf{G_D} + \mathbf{G_{DS}} + r\mathbf{G_{SD}} + \mathbf{G_S})\boldsymbol{\beta_S}, \quad \text{(A4)}$$

which is an analog of the trait-based equation (10) and a multivariate version of the general equation in table 4 of Bijma and Wade (2008) when $n = 2$.

The equivalence of equations (10) and (A4) can be demonstrated by substituting the definitions of $\mathbf{G_D}$, $\mathbf{G_{DS}}$, $\mathbf{G_{SD}}$, and $\mathbf{G_S}$ derived by McGlothlin and Brodie (2009). When assortment of individuals occurs based on specific traits, equation (A4) can be defined in terms of relatedness matrices,

$$\Delta\bar{\mathbf{z}} = \left(\mathbf{G_D} + \mathbf{G_{DS}}\mathbf{R_{DS}^T} + \mathbf{G_{SD}} + \mathbf{G_S}\mathbf{R_S^T}\right)\boldsymbol{\beta_N} + \left(\mathbf{G_D}\mathbf{R_D^T} + \mathbf{G_{DS}} + \mathbf{G_{SD}}\mathbf{R_{SD}^T} + \mathbf{G_S}\right)\boldsymbol{\beta_S}, \quad \text{(A5)}$$

where each relatedness matrix is composed of partial regression coefficients relating the direct and/or social breeding values of the focal individual and its social partner. These matrices may be estimated empirically using best linear unbiased predictors of breeding values from an animal model analysis (Kruuk 2004). In general, these relatedness matrices are not equal to $\mathbf{R}$ from the trait-based model when IGEs are present. However, when all relevant social traits have been measured, it can be shown that $\mathbf{R_{DS}^T} = \mathbf{R_S^T}$ and $\mathbf{R_D^T} = \mathbf{R_{SD}^T}$.

The equivalence of the variance-components and trait-based models means either model may predict the correct multivariate response to selection, if all relevant traits are included. Both models demonstrate that a nonzero $\mathbf{C_{Az'}}$ may arise from relatedness, IGEs, or both. However, the symmetry between relatedness and IGEs in their effects on the response to selection is as not apparent in the variance-components model. Empirically, the variance-components approach is advantageous because specific interacting phenotypes need not be identified a priori to predict responses to selection. If a set of candidate traits can be identified, the equivalences between the two theoretical frameworks can be used to measure indirect genetic effects of specific traits (Galloway et al. 2009; McGlothlin and Brodie 2009).

Appendix B

IGEs AND SOCIAL SELECTION IN LARGER GROUPS

Here, we derive the equation for response to social selection using the model of IGEs in larger groups developed by McGlothlin and Brodie (2009), which assumes nonoverlapping groups of equal size. This treatment generalizes the results of Agrawal et al. (2001). However, note that we consider the elements of $\mathbf{G}$ to represent the parameters that could be measured in a current population considered globally, rather than those of a hypothetically panmictic population (see Bijma et al. 2007a for a discussion of this distinction). We also consider only linear IGEs, ignoring the nonlinear effects discussed by Agrawal et al. (2001).

The phenotype of a focal individual can be represented as the sum of its direct genetic and environmental effects and the sum of the social effects of all the members of its group,

$$\mathbf{z} = \mathbf{a} + \mathbf{e} + (n-1)\boldsymbol{\Psi}\bar{\mathbf{z}}', \quad \text{(B1)}$$

where $\bar{\mathbf{z}}'$ represents the mean phenotype of the social group excluding the focal individual and n represents the group size. Each individual is affected by the focal individual as well as all other group members. Using superscript $\mathbf{i}$ to designate a particular social interactant,

$$\mathbf{z'^i} = \mathbf{a'^i} + \mathbf{e'^i} + (n-1)\boldsymbol{\Psi}\bar{\mathbf{z}}' - \boldsymbol{\Psi}\mathbf{z'^i} + \boldsymbol{\Psi}\mathbf{z}. \quad \text{(B2)}$$

We can solve for $\bar{\mathbf{z}}'$ by taking the expectation of equation (B2):

$$\bar{\mathbf{z}}' = \bar{\mathbf{a}}' + \bar{\mathbf{e}}' + (n-1)\boldsymbol{\Psi}\bar{\mathbf{z}}' - \boldsymbol{\Psi}\bar{\mathbf{z}}' + \boldsymbol{\Psi}\mathbf{z}. \quad \text{(B3)}$$

To solve for an explicit definition of $\mathbf{z}$, we first note that

$$(n-1)\boldsymbol{\Psi}\bar{\mathbf{z}}' = \mathbf{z} - (\mathbf{a} + \mathbf{e}),$$

and therefore

$$\bar{\mathbf{z}}' = \bar{\mathbf{a}}' + \bar{\mathbf{e}}' + [\mathbf{z} - (\mathbf{a} + \mathbf{e})] - (n-1)^{-1}[\mathbf{z} - (\mathbf{a} + \mathbf{e})] + \boldsymbol{\Psi}\mathbf{z}. \quad \text{(B4)}$$

Now we can substitute this definition of $\bar{\mathbf{z}}'$ into the implicit definition of $\mathbf{z}$.

$$\mathbf{z} = \mathbf{a} + \mathbf{e} + (n-1)\boldsymbol{\Psi}(\bar{\mathbf{a}}' + \bar{\mathbf{e}}') + (n-1)\boldsymbol{\Psi}[\mathbf{z} - (\mathbf{a} + \mathbf{e})] - \boldsymbol{\Psi}[\mathbf{z} - (\mathbf{a} + \mathbf{e})] + (n-1)\boldsymbol{\Psi}\boldsymbol{\Psi}\mathbf{z}.$$

Simplifying, we find

$$\mathbf{z} = \mathbf{a} + \mathbf{e} + (n-1)\boldsymbol{\Psi}(\bar{\mathbf{a}}' + \bar{\mathbf{e}}') + (n-2)\boldsymbol{\Psi}[\mathbf{z} - (\mathbf{a} + \mathbf{e})] + (n-1)\boldsymbol{\Psi}\boldsymbol{\Psi}\mathbf{z}$$

and

$$\mathbf{z} = [\mathbf{I} - (n-2)\boldsymbol{\Psi} - (n-1)\boldsymbol{\Psi}\boldsymbol{\Psi}]^{-1} \times [\mathbf{a} + \mathbf{e} + (n-1)\boldsymbol{\Psi}(\bar{\mathbf{a}}' + \bar{\mathbf{e}}') - (n-2)\boldsymbol{\Psi}(\mathbf{a} + \mathbf{e})]. \quad \text{(B5)}$$

Using a similar process, we can explicitly define $\bar{\mathbf{z}}'$:

$$\bar{\mathbf{z}}' = \bar{\mathbf{a}}' + \bar{\mathbf{e}}' + (n-2)\boldsymbol{\Psi}\bar{\mathbf{z}}' + \boldsymbol{\Psi}[\mathbf{a} + \mathbf{e} + (n-1)\boldsymbol{\Psi}\bar{\mathbf{z}}']$$

and

$$\bar{\mathbf{z}}' = [\mathbf{I} - (n-2)\boldsymbol{\Psi} - (n-1)\boldsymbol{\Psi}\boldsymbol{\Psi}]^{-1}[\bar{\mathbf{a}}' + \bar{\mathbf{e}}' + \boldsymbol{\Psi}(\mathbf{a} + \mathbf{e})]. \tag{B6}$$

To calculate the total breeding value $\mathbf{A}$, we take the expectation of the equation (B1) over all social groups, $\bar{\bar{\mathbf{z}}} = \bar{\bar{\mathbf{a}}} + (n-1)\boldsymbol{\Psi}\bar{\bar{\mathbf{z}}}$ or $\bar{\bar{\mathbf{z}}} = [\mathbf{I} - (n-1)\boldsymbol{\Psi}]^{-1}\bar{\bar{\mathbf{a}}}$, and then define total breeding value as each individual's contribution to the population mean,

$$\mathbf{A} = [\mathbf{I} - (n-1)\boldsymbol{\Psi}]^{-1}\mathbf{a}. \tag{B7}$$

We can solve for $\Delta\bar{\bar{\mathbf{z}}}$ by substituting equations (B5–B7) into equation (17), resulting in equation (18). This result assumes relatedness between the focal individual and the average group member is uniform across traits; this assumption can be relaxed by replacing all r with $\mathbf{R}^{\mathrm{T}}$.

Similarly, in the variance-components framework, the total breeding value is defined as a sum of direct and social components

$$\mathbf{A} = \mathbf{a_D} + (n-1)\mathbf{a_S}. \tag{B8}$$

The focal and mean interactant phenotypes are defined as

$$\mathbf{z} = \mathbf{a_D} + \mathbf{e_D} + (n-1)(\bar{\mathbf{a}}'_{\mathbf{S}} + \bar{\mathbf{e}}'_{\mathbf{S}}) \tag{B9}$$

and

$$\bar{\mathbf{z}}' = \bar{\mathbf{a}}'_{\mathbf{D}} + \bar{\mathbf{e}}'_{\mathbf{D}} + (n-2)(\bar{\mathbf{a}}'_{\mathbf{S}} + \bar{\mathbf{e}}'_{\mathbf{S}}) + \mathbf{a_S} + \mathbf{e_S}. \tag{B10}$$

Substituting equations (B8–B10) into equation (17) and assuming uniform relatedness across traits gives

$$\begin{aligned}\Delta\bar{\bar{\mathbf{z}}} = {} & [\mathbf{G_D} + r(n-1)\mathbf{G_{DS}} + (n-1)\mathbf{G_{SD}} + r(n-1)^2\mathbf{G_S}]\boldsymbol{\beta}_{\mathbf{N}} \\ & + (n-1)[r\mathbf{G_D} + (\mathbf{I} + r(n-2))\mathbf{G_{DS}} \\ & + r(n-1)\mathbf{G_{SD}} + (\mathbf{I} + r(n-2))\mathbf{G_S}]\boldsymbol{\beta}_{\mathbf{S}}.\end{aligned} \tag{B11}$$

This is the multivariate version of the general equation from table 4 in Bijma and Wade (2008). Substitution of the equivalences in equations (25a-d) of McGlothlin and Brodie (2009) can be used to demonstrate equivalence of the two frameworks. Nonuniform relatedness can be dealt with as in the text by defining matrices $\mathbf{R_D}$, $\mathbf{R_{DS}}$, $\mathbf{R_{SD}}$, and $\mathbf{R_S}$.