

INTERACTING PHENOTYPES AND THE EVOLUTIONARY PROCESS: I. DIRECT AND INDIRECT GENETIC EFFECTS OF SOCIAL INTERACTIONS

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Abstract.—Interacting phenotypes are traits whose expression is affected by interactions with conspecifics. Commonly-studied interacting phenotypes include aggression, courtship, and communication. More extreme examples of interacting phenotypes—traits that exist exclusively as a product of interactions—include social dominance, intraspecific competitive ability, and mating systems. We adopt a quantitative genetic approach to assess genetic influences on interacting phenotypes. We partition genetic and environmental effects so that traits in conspecifics that influence the expression of interacting phenotypes are a component of the environment. When the trait having the effect is heritable, the environmental influence arising from the interaction has a genetic basis and can be incorporated as an indirect genetic effect. However, because it has a genetic basis, this environmental component can evolve. Therefore, to consider the evolution of interacting phenotypes we simultaneously consider changes in the direct genetic contributions to a trait (as a standard quantitative genetic approach would evaluate) as well as changes in the environmental (indirect genetic) contribution to the phenotype. We then explore the ramifications of this model of inheritance on the evolution of interacting phenotypes. The relative rate of evolution in interacting phenotypes can be quite different from that predicted by a standard quantitative genetic analysis. Phenotypic evolution is greatly enhanced or inhibited depending on the nature of the direct and indirect genetic effects. Further, unlike most models of phenotypic evolution, a lack of variation in direct genetic effects does not preclude evolution if there is genetic variance in the indirect genetic contributions. The available empirical evidence regarding the evolution of behavior expressed in interactions, although limited, supports the predictions of our model.

Key words.—Evolutionary rates, extended phenotypes, phenotypic evolution, quantitative genetics, social behavior.

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Many evolutionarily important characters can be difficult to define as explicit quantitative phenotypes, especially those that are only expressed during social interactions among conspecifics. Such traits are unique in that they are determined, in part, by the phenotypes of other individuals. Many authors have predicted that traits expressed during social interactions evolve more rapidly than, and even lead, the evolution of other types of traits (Fisher 1915, 1958; Mayr 1958, 1960, 1963; West-Eberhard 1979, 1983, 1984; Lande 1981; Kirkpatrick 1982; Moore et al., in press). Examples of traits in which the expression of the phenotype depends, at least in part, on an interaction include behavior such as aggression, territoriality, altruism and courtship (Huntingford and Turner 1987; Dewsbury 1988; Eberhard 1994, 1996; Meffert 1995). The expression of non behavioral traits, such as pollen tube growth in plants (Wilson 1994) or copulatory structures and genitalia (Eberhard 1985, 1996; Wilson 1994), can also be affected by interactions. Even more extreme are traits that cannot be defined outside of interactions such as social dominance, intraspecific competition, and mating systems. The common feature of such characters is that the interactions among individuals help determine the phenotype (Dawkins and Krebs 1978; Dawkins 1982; Krebs and Dawkins 1984; Meffert 1995).

We use the term “interacting phenotypes” to describe traits that require or are influenced by interactions with a conspecific social partner or neighbor. Dawkins (1982) also recognized the importance of interactions and used the term “extended phenotype” to describe the effects of genes on

phenotypes other than their own. Dawkins noted that extended phenotypes are unique because they provide both an environmental effect and selection. However, Dawkins extended the notion of extended phenotypes to any interaction, including “effects on the world at large” (Dawkins, 1982, p. 5). Here we wish to limit our discussion to the effects of individuals on conspecifics. Thus, we prefer the term “interacting phenotype.”

Although it has been recognized for some time that interacting phenotypes are unique, there is substantial disagreement over how such traits should be interpreted. An illustrative example of this debate is the controversy over the study of genetic effects on social dominance. Because social dominance cannot be defined outside the context of an interaction, it has been described as an emergent property that is unrelated to individuals (Capitanio 1991, 1993; Barrette 1993). However, if social dominance is to evolve, then it must be somehow influenced by inheritance and selection. This view has led to the argument that the heritability or genetics of dominance can be examined (Fuller and Hahn 1976; Hughes 1989; Dewsbury 1991, 1993; Moore 1991, 1993; Hahn and Schanz 1996). Given such contradictory approaches, how are we to describe the inheritance and evolution of traits such as social dominance that require social interactions for their expression? If the genes can only influence the individual phenotype of the body in which they exist, then we are left with an inability to define genes’ influences on traits that cannot be defined outside of a social context.

Understanding the evolution of interacting phenotypes is further complicated because interacting phenotypes are simultaneously environments and evolving traits, thus the en-

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vironment itself can evolve. Further, interacting phenotypes can generate selection because they are expressed in interactions among individuals. Consolidating all of these features into a single family of models is essential if we are to elucidate the evolution of interacting phenotypes. In this paper we begin that process by examining how models of inheritance can be reconciled with this view of interacting phenotypes.

Previous theory that attempts to describe the evolution of characters expressed during interactions has focused on the selection resulting from (West-Eberhard 1979, 1983, 1984, 1989), or fitness consequences of (i.e., optimality; Maynard Smith 1982; Grafen 1991) interactions. This emphasis reflects, in part, the acknowledged difficulty in explaining how social behavior can be adaptive for individuals under many circumstances (Darwin 1859, 1871; Mayr 1963; Hamilton 1996). While both optimality-oriented and selection-oriented approaches have led to a greater understanding of the fitness consequences of interacting phenotypes, they only consider half of the evolutionary equation (Moore and Boake 1994). Given that the effects of selection are filtered through the system of inheritance, it is essential to investigate the role that genetics may play in the evolution of phenotypes that require interactions to be expressed.

Although Dawkins (1982) advocates a genetic view of extended phenotypes, he presents no formal treatment of the genetics of interacting phenotypes. However, a genetic perspective on social interactions among unrelated individuals is not completely lacking. Meffert (1995) recently presented a model using Monte Carlo simulations of mating behavior and genetic influences on male and female behavior. In her one-locus (in each sex) two allele model she found that considering the environmental effect of the mating partner's phenotype, or the potential for genotype \times genotype effects resulting from interactions, provided a better prediction of the parent-offspring covariances she measured (Meffert 1995). Other models that have considered interacting phenotypes have focused either on interactions among related individuals (i.e., maternal effects models; Cheverud 1984; Riska et al. 1985; Lynch 1987; Kirkpatrick and Lande 1989, 1992; Lande and Kirkpatrick 1990; Cheverud and Moore 1994; Wade, in press) or have not considered phenotypic evolution (Griffing 1967, 1977, 1981; Cockerham and Burrows 1971; Cockerham et al. 1972).

These models that consider how interactions among individuals change inheritance reveal the importance of indirect genetic effects. Indirect genetic effects are genetically-based environmental influences and are generated whenever the phenotype of one individual acts as an environment for another (Moore et al. in press). In this paper we provide a model of the phenotypic evolution of traits expressed during interactions among unrelated individuals. We adopt the approach first used by Kirkpatrick and Lande (1989) to model the effects of interactions between parents and offspring. However, our general model describes the indirect genetic effects that arise whenever phenotypes are influenced by interactions with unrelated conspecifics. We examine traits that are influenced by interactions as well as those that act as environments for other traits—in some cases a single trait may play both roles. By taking a quantitative genetic approach, we consider

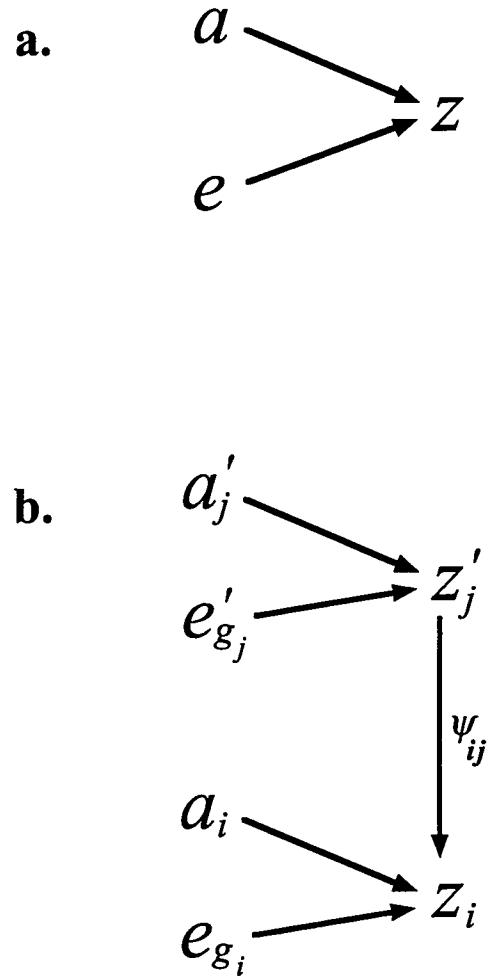


FIG. 1. Diagrams illustrating the genetic and environmental contributions to phenotypes. Figure 1a illustrates the contributions to non-interacting phenotypes z where each phenotype is influenced solely by environmental, e , and additive genetic, a , components. Figure 1b illustrates the contributions to an interacting phenotypes z_i and a non-interacting phenotype z_j where the expression of z_i is influenced by being expressed during an interaction with z_j .

the process of inheritance separately from the relationship between traits and fitness. Our model is thereby complementary to previous work that has investigated selection on interacting phenotypes.

INHERITANCE OF INTERACTING PHENOTYPES

In standard quantitative genetic models, phenotypes of individuals, z , are partitioned into component additive genetic, a , and environmental, e , effects (Falconer and Mackay 1996):

$$z = a + e \quad (1)$$

(Fig. 1a). Equation (1) describes simple Mendelian inheritance of direct genetic effects (Fisher 1918) and forms the foundation for all of quantitative genetics. Other partitionings are possible; in particular, specific environmental subdivisions as well as other genetic effects such as dominance and epistasis are often examined (Falconer and Mackay 1996).

By definition, the expression of an interacting phenotype by one individual is influenced by the characteristics of a

second individual. Thus, this second individual can be thought of as providing an environment for the first individual (Griffing 1977; Moore 1993; Meffert 1995). Mathematically, this can be expressed by partitioning the environmental deviation, e , into two parts. We now have the contribution of the general environmental effect, e_{gi} , and the environment contributed by phenotype z_j of an interacting individual, e_{zj} , as well as an additive genetic effect, a_i , (i.e., a direct genetic effect), on the phenotype z_i in the first individual, z_i :

$$z_i = a_i + e_{gi} + e_{zj} \quad (2a)$$

Because e_{zj} is determined by the phenotype of another individual, we can substitute the definition for the phenotype z_j in the second individual:

$$z_i = a_i + e_{gi} + \Psi_{ij}z'_j \quad (2b)$$

where $\Psi_{ij}z'_j$ is the effect of phenotype z'_j in another individual that influences the expression of z_i in the first individual (Fig. 1b). The interaction effect coefficient, Ψ_{ij} , is a path coefficient that describes the extent that z_i changes as a result of interacting with z'_j .

Because our model considers the expression of multiple traits in multiple individuals, we use a prime, ', throughout to denote a trait expressed by the social partner. However, the genes for all traits are present in all individuals, and all traits can be expressed by all individuals. Within the population individuals can be both the social partner and the focal individual. Traits expressed by the focal individual, or in the population, lack a prime.

The interaction effect coefficient is defined as the partial regression coefficient of z_i on z'_j (i.e., the effect of z'_j on z_i holding all other sources of variation constant). In practice, Ψ_{ij} , describes the mean deviation from a predicted value of z_i , (i.e., the amount z_i is changed from its expected expression in the absence of an interaction). When z_i and z_j are standardized variables ($\bar{x} = 0$, $SD = 1$) this parameter is equivalent to a path coefficient (Fig. 1b) and therefore takes on any value from -1 to 1 . Here, we assume all variables are standardized, which makes interpretations of Ψ_{ij} more intuitive. For example, when $\Psi_{ij} = 0$, equation (2b) reduces to the classic quantitative genetic expression presented in equation (1). Of course $\Psi_{ij} = 0$ is a very unlikely condition for a trait that requires a social interaction to be expressed. Finally, for the models we present here, we assume that Ψ_{ij} is a fixed population parameter and does not differ among genotypes.

This model of inheritance assumes that every individual engages in a single pairwise interaction within a population. Further, it assumes that both z_i and z_j are expressed in every individual.

We can modify equation (2b) to accommodate n additional traits expressed within the same social partner:

$$z_i = a_i + e_{gi} + \sum_{j=1}^n \Psi_{ij}z'_j \quad (3)$$

To model multiple pairwise interactions, each with a different partner, each interaction can be considered to result in the expression of a different, or new, phenotype in the focal individual. This is equivalent to treating a trait measured under varied environmental conditions, or morphology mea-

sured at different points in development, as a different character (Falconer and Mackay 1996, p. 322). With this logic, we can then model multiple interactions using a multivariate formulation of inheritance and our models; such a presentation is developed below.

Because z'_j is itself a phenotype it too is influenced by genetic and environmental effects. The contribution of the z'_j to the phenotype z_i results in indirect genetic effects because the genetic component of z'_j effects the expression of z_i . Below, we illustrate how the indirect genetic effects generated among traits expressed during interactions might alter the pattern of inheritance and thereby the response to selection.

EVOLUTION OF INTERACTING PHENOTYPES—MODELS

Having defined inheritance for interacting phenotypes, we can now derive equations for phenotypic evolution. The primary complication for understanding evolutionary change of traits expressed in interactions is that the mean environment (i.e., the other interacting phenotype) can change in the same time frame that the mean additive genetic value for the trait changes. Thus, models of evolutionary change must consider changes in the environment provided by unrelated conspecifics that act as social partners.

Interactions between individuals can take several forms, and below we outline three common categories of interactions where interacting phenotypes are expressed. We consider interactions between two individuals, each expressing a single character, and build from a simple case to more complex situations. In the first case, two different traits are expressed in each individual but the expression of only one of the traits is affected by the interaction (i.e., only one trait is an interacting phenotype). This can be described as an interaction with non-reciprocal effects. The next two examples concern interactions with reciprocal effects. In the second case, each interacting individual expresses a different trait, and both traits reciprocally affect each other (i.e., both traits are interacting phenotypes). In the third example, each interacting individual expresses the same trait, and this trait reciprocally affects itself (i.e., an interacting phenotype that affects itself). Heuristic examples drawn from behavior expressed during social interactions are offered for each case. We modify equation (2b) to describe a specific univariate model of inheritance for each case, developed from the perspective of the focal individual, then derive the equations for the mean phenotypes and evolutionary change in the mean phenotypes in the population. Finally, we present a general multivariate model so that all conditions and types of traits may be considered simultaneously. In each model we assume that interactions occur at random among individuals (i.e. random associations among individuals) and that all individuals can express all traits (i.e., both z_i and z_j). Although our examples are drawn from social behavior, our approach is general and applicable to any interacting phenotype.

Interactions with Nonreciprocal Effects

Many phenotypes are fixed prior to an interaction but still influence the expression of a different trait in the other individual. A common example is the effect of body size on

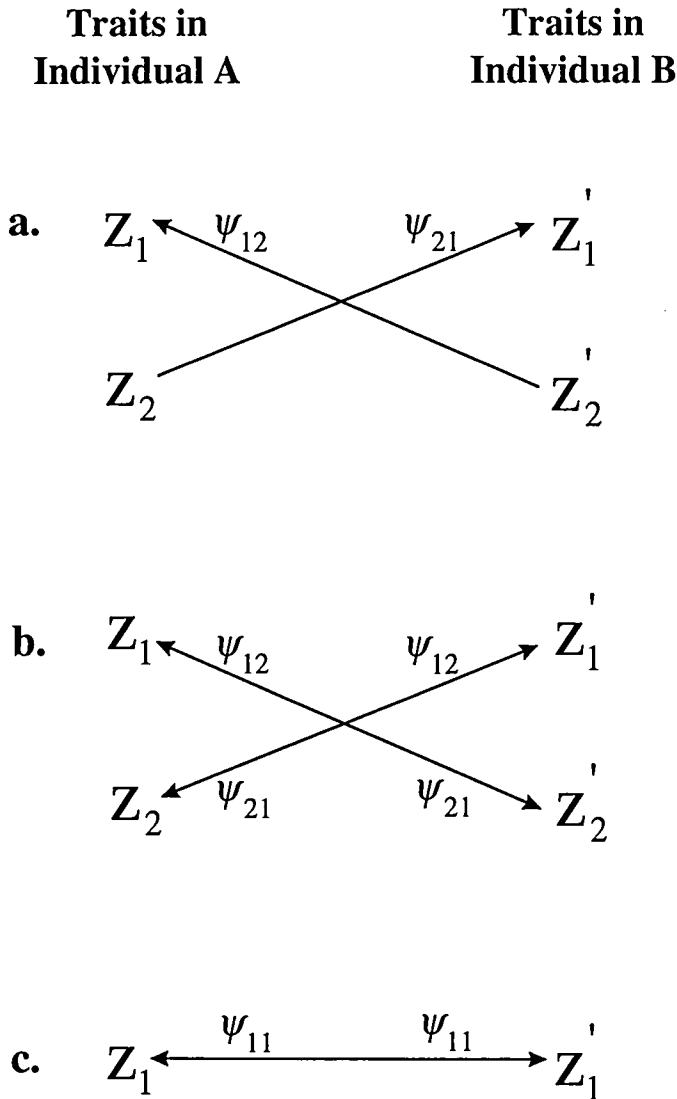


FIG. 2. Diagrams of specific univariate interactions among phenotypes. For each example, each trait is expressed in both interacting individuals. (a) An interaction with non-reciprocal effects, where the expression of a trait in one individual (z_1) is influenced by a second trait in another individual (z_2 ; the second trait is unaffected by the interaction). (b) An interaction with reciprocal effects between different traits (e.g., z_1 and z_2), where z_1 in one individual is affected by z_2 in the second individual and vice versa. (c) An interaction with reciprocal effects between the same trait in two individuals (z_1 and z_1).

aggression. Individuals often mediate their aggression based on the body size of their opponent (e.g., Thornhill 1983; Huntingford and Turner 1987; Maynard Smith and Brown 1987). Under these conditions, the phenotype z_1 is affected by the phenotype z_2 expressed by a different individual (i.e., z_2'), but z_2 does not reflect the effects of the interaction (i.e., z_1' ; Fig. 2a):

$$z_1 = a_1 + e_1 + \Psi_{12}z_2'. \quad (4)$$

Because z_2' is unaffected by the interaction, its value is described by the standard quantitative genetic equation, equation (1). Substituting for z_2' , the equations simplify so that

$$z_1 = a_1 + e_1 + \Psi_{12}a_2' + \Psi_{12}e_2'. \quad (5a)$$

For the trait that is a non-interacting phenotype, we have the standard expression for a character, from equation (1):

$$z_2 = a_2 + e_2. \quad (5b)$$

We can now define the mean values for the phenotypes by taking the expectations:

$$\bar{z}_1 = \bar{a}_1 + \Psi_{12}\bar{a}_2, \quad (6a)$$

and for the unaffected trait

$$\bar{z}_2 = \bar{a}_2. \quad (6b)$$

The mean value of a trait influenced by an interaction depends not only on direct genetic effects, but also on indirect genetic effects. The mean of the interacting phenotype z_1 therefore includes the mean additive genetic value \bar{a}_1 plus the breeding value of the environmental effect trait weighted by the degree that environment affects the expression of the trait ($\Psi_{12}\bar{a}_2$).

Making standard quantitative genetic assumptions (Falconer and Mackay 1996), from these equations of phenotypic influences we define variance components to evaluate the potential for evolutionary change in a phenotype. Environmental effects are assumed to be independent and normally distributed with a mean of zero and variance E . Further assuming that environmental effects are independent of the additive genetic effect, the overall phenotypic variance, P , is simply the sum of the additive genetic variance, G , and environmental variance E . Note, however, that indirect genetic effects can now contribute to P (Appendix). In order to evaluate evolutionary changes in the trait means, the variances P and G are assumed to remain constant over time (i.e. selection is weak and many loci contribute to the genetic variance; Bulmer 1985). Although this latter assumption has been questioned (e.g., Barton and Turelli 1989), it is made to permit us to investigate short-term evolution (Lande 1979). For simplicity all genes are assumed to be inherited autosomally.

Evolutionary changes in quantitative characters can be predicted by selection, β , acting through the covariance between the breeding value of a trait and the phenotypic value for that trait ($Cov[A, z]$; Falconer and Mackay 1996; for a detailed example of how this approach is applied to interacting phenotypes see Cheverud and Moore [1994]). The advantage of this approach is that the breeding value, A , which equals the sum of the average effects of all alleles carried by an individual within a population (Falconer and Mackay 1996; pp. 114–115), allows us to consider the more complicated inheritance described by equation (5a). When individuals express interacting phenotypes, the breeding value for an individual is more than just the direct additive genetic value for a trait; the breeding value includes the indirect additive value of the other phenotype as well (i.e., $A = a_1 + \Psi_{12}a_2$). Assuming no genotype/environment covariance, we can simultaneously model both direct and correlated responses to selection on the covariance between this breeding value and the two traits under consideration:

$$\Delta\bar{z}_1 = [Cov(a_1 + \Psi_{12}a_2, z_1)\beta_1 + Cov(a_1 + \Psi_{12}a_2, z_2)\beta_2]. \quad (7)$$

Substituting equation (5a) for z_1 and equation (5b) for z_2 , and

taking the covariances, the equation for total evolutionary change is:

$$\Delta \bar{z}_1 = [(G_{11} + \Psi_{12}G_{12})\beta_1 + (G_{12} + \Psi_{12}G_{22})\beta_2]. \quad (8)$$

Equation (8) describes responses to selection from both direct selection on the trait of interest, β_1 , and indirect selection on a potentially-correlated character, β_2 . G_{ii} is the genetic variance for z_i and G_{ij} is the genetic covariance between the traits. Selection is defined by the gradient $\beta_i = s_i/P_{ii}$ where P_{ii} is the phenotypic variance, and s_i is the selection differential (Lande and Arnold 1983). Note, however, that the translation of selection during interactions into a simple selection gradient, β , is not always straightforward because interactions change the phenotypic variance-covariance structure (Appendix) and may even generate covariances among individuals in interactions (Wolf et al., unpubl. manuscript).

Equation (8) reveals two unique aspects of the evolution of interacting phenotypes. First, selection, β_2 , directly affecting the trait that serves as an environment, z_2 , causes a change in the interacting phenotype, z_1 . Second, the response to direct selection on the interacting phenotype itself is influenced by the genetic covariance between the traits. Both of these new components of evolutionary response arise because of indirect genetic effects and are mediated through the strength of the interaction effect coefficient—the greater the effect of the interaction, the more the expected response to selection differs from the standard models under Mendelian inheritance. In contrast, for a trait that acts only as an environment, no part of its phenotypic expression is determined by another trait. Thus, the change in z_2 is described by the standard equation for direct and correlated responses to selection ($\Delta \bar{z}_2 = [(G_{22})\beta_2 + (G_{21})\beta_1]$; Lande 1979).

Interactions with Reciprocal Effects on Two Different Traits

Social dominance is a classic example of a social interaction where the two interacting individuals each express traits that are affected by the expression of the other trait (Moore 1993). During ritualized social contests leading to the formation of dominance hierarchies, individuals often exhibit specific agonistic behaviors associated with social status (e.g., offensive behaviors, displays by dominant individuals, and defensive postures, escape, displays by subordinate individuals). The level of a subordinate response to a dominant act often mediates the degree that dominant behavior is expressed. Likewise, the degree that subordinate behavior is expressed often depends on the level of the dominant behavior expressed by the dominant individual. Note that dominant behaviors and subordinate behaviors are different characters, not just differences in the degree of aggression being expressed. All individuals have the potential to express both dominant and subordinate behavior (Fig. 2b).

In this situation, the traits in a focal individual can be defined as

$$z_1 = a_1 + e_1 + \Psi_{12}z_2' \quad (9a)$$

$$z_2 = a_2 + e_2 + \Psi_{21}z_1' \quad (9b)$$

by substitution into equation (2b). The traits in the opponent (z_1' and z_2') can be defined by similar equations. By substituting for z_1' and z_2' we derive alternative equations for z_1 and z_2 strictly in terms of additive genetic and environmental effects:

$$z_1 = \frac{a_1 + e_1 + \Psi_{12}a_2' + \Psi_{12}e_2'}{(1 - \Psi_{12}\Psi_{21})}, \quad (10a)$$

$$z_2 = \frac{a_2 + e_2 + \Psi_{21}a_1' + \Psi_{21}e_1'}{(1 - \Psi_{21}\Psi_{12})}. \quad (10b)$$

Taking the expectation the mean values for the phenotypes are

$$\bar{z}_1 = \frac{\bar{a}_1 + \Psi_{12}\bar{a}_2}{1 - \Psi_{12}\Psi_{21}}, \quad (11a)$$

$$\bar{z}_2 = \frac{\bar{a}_2 + \Psi_{21}\bar{a}_1}{1 - \Psi_{21}\Psi_{12}}. \quad (11b)$$

Again the mean value of a trait depends not only on direct genetic effects but also on indirect genetic effects. The mean of each trait now has three components: the first is the mean additive genetic value (\bar{a}_1 in the case of \bar{z}_1). The second is the mean additive genetic value of the environmental effect weighted by the degree that environment affects the expression of the trait ($\Psi_{12}\bar{a}_2$ in the case of \bar{z}_1). The last accounts for the feedback of the expression of each trait on the other trait ($1/(1 - \Psi_{12}\Psi_{21})$ in the case of \bar{z}_1). This feedback loop occurs because any change in the value of the first trait will affect the mean value of the second trait, which again feeds back on the first trait. Note that the values of $|\Psi|$ must be less than one for trait values to remain finite.

We can use the expression for evolutionary change described by equation (7) and, making the same assumptions, substitute into this definitions of the phenotypes from equations (10a) and (10b) to solve for direct and correlated responses to selection. However, because both traits are interacting phenotypes, the breeding value has to take into account that both characters reflect the influence of the other character. The breeding value under these conditions, for a trait with reciprocal interactions, is therefore $A = a_1 + \Psi_{12}a_2/(1 - \Psi_{12}\Psi_{21})$. Substituting this value into equation (7) and substituting equation (10a) for z_1 and (10b) for z_2 , the total response to selection in a single generation for two different traits expressed with bi-directional interactions becomes

$$\Delta \bar{z}_1 = \left(\frac{1}{1 - \Psi_{12}\Psi_{21}} \right)^2 \times [(G_{11} + \Psi_{12}G_{12})\beta_1 + (G_{12} + \Psi_{12}G_{22})\beta_2]. \quad (12a)$$

The same logic holds for the other character expressed in this reciprocal interaction:

$$\Delta \bar{z}_2 = \left(\frac{1}{1 - \Psi_{21}\Psi_{12}} \right)^2 \times [(G_{22} + \Psi_{21}G_{21})\beta_2 + (G_{21} + \Psi_{21}G_{11})\beta_1]. \quad (12b)$$

In both equations G_{ii} and G_{ij} are again the genetic variances and covariances, respectively, and β_i is the selection gradient directly acting on a trait.

As in the non-reciprocal example, responses to selection are expected to differ from the standard model of evolution-

ary change. However, an additional effect on the rate of change between generations occurs because of the presence of reciprocal effects of the interaction and non-zero interaction effect coefficients for both traits. The relative rate of evolution can be much faster (whenever the effects are of the same sign) or slower (whenever the effects are of different sign) than in traits that are expressed independently of interactions (Fig. 3a). For example, assuming moderate values and the same sign for the interaction effect coefficients (e.g., $\Psi_{12} = \Psi_{21} = 0.75$), evolution will occur over five times as fast as would be expected without the effects of the interaction. Interaction effect coefficients of the same sign are predicted for many social interactions including the example of dominance, where higher levels of subordinate displays are expected to increase the expression of dominant behavior and vice versa. The effect of the interaction effect coefficient increases as it approaches 1 (Fig. 3a). If the interaction effect coefficient is zero our model reduces to the standard quantitative genetic model for evolutionary change (Lande 1979).

Interaction with Reciprocal Effects on a Single Trait

Our final example involves social interactions where the same trait is expressed in different individuals, each affecting the other (Fig. 2c). A common example is aggression. The level of aggression displayed by one individual is often affected by the level of aggression displayed by the other individual with which it interacts (Huntingford and Turner 1987). Under these conditions, only a single trait is expressed

$$z_1 = a_1 + e_1 + \Psi_{11}z'_1. \quad (13)$$

Solving as before:

$$z_1 = \frac{a_1 + e_1 + \Psi_{11}a'_1 + \Psi_{11}e'_1}{(1 - \Psi_{11}\Psi_{11})}. \quad (14)$$

The mean of the trait can be expressed as

$$\bar{z}_1 = \frac{\bar{a}_1}{1 - \Psi_{11}}. \quad (15)$$

The breeding value for an interacting phenotype influenced by itself is $A = a_1/(1 - \Psi_{11})$. Solving for direct and correlated selection on traits 1 and 2 using equations (7) and (14) with only a single interacting phenotype, using the appropriate breeding value we can substitute as before to get an expression for the total response to selection:

$$\Delta\bar{z}_1 = \left(\frac{1}{1 - \Psi_{11}^2} \right)^2 [(G_{11} + \Psi_{11}G_{11})\beta_1] \quad (16a)$$

or, collecting terms,

$$\Delta\bar{z}_1 = \left(\frac{1}{1 - \Psi_{11}^2} \right) \left(\frac{1}{1 - \Psi_{11}} \right) [G_{11}\beta_1]. \quad (16b)$$

Again, the value of $|\Psi|$ must be less than one for finite trait values.

The phenotypic evolution of this trait can be remarkably rapid. Whenever reciprocal interactions involve the same trait, the influence of the interaction effect coefficient is increased because both individuals experience the effect simultaneously. The result is that, given even a moderate in-

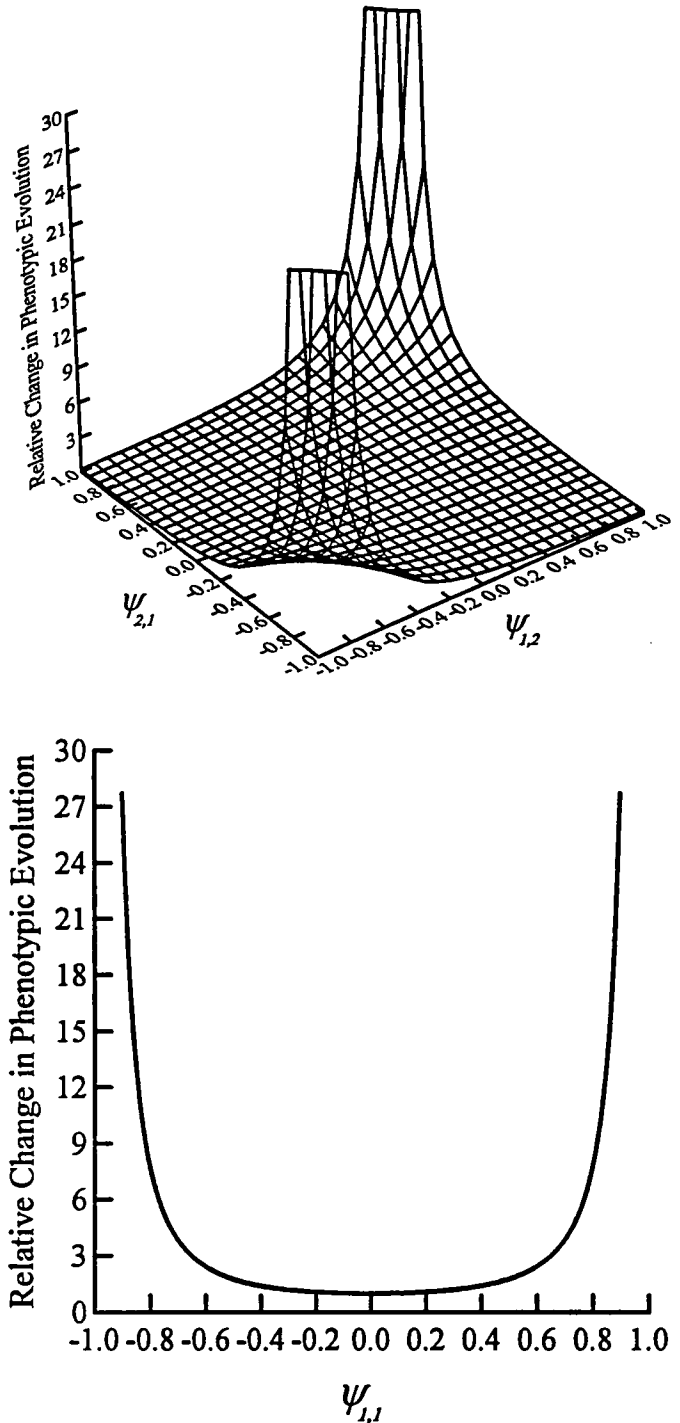


FIG. 3. The importance of the interaction effect coefficient, Ψ_{ij} , on relative rates of evolution within interactions with reciprocal effects. The interaction effect coefficient can be positive or negative. When the influence of the interaction is of opposing sign for two traits, the effect cancels out. However, whenever both interactions are of the same sign, the interaction increases the relative rate of evolution. This effect accelerates toward infinity as $|\Psi_{ij}|$ increases. (a) An interaction with reciprocal effects involving two different characters expressed in different individuals. (b) An interaction with reciprocal effects involving the same character expressed in both social partners.

teraction effect coefficient, the relative increase in the rate of evolution is accelerated (Fig. 3b). For example, if $\Psi_{11} = 0.75$, the response to selection in a single generation will be over nine times as great as that expected in the absence of an interaction. Again, this effect accelerates as the interaction effect coefficient approaches 1 (Fig. 3b). As before, this effect is in addition to the consequences of indirect genetic effects described for interactions with non-reciprocal effects.

Multivariate Evolution

Interactions are likely to involve the expression of many different interacting phenotypes. For example, when an individual interacts with several social partners in succession, the behavior expressed during each pairwise interaction can be considered a different phenotype. Within agonistic interactions there are often several characters that are expressed, including overt aggression, multiple dominant and subordinate signals, and effects of body size. Courtship is another commonly-analyzed social behavior that typically involves both a series of behavioral interactions, signals, and the influence of fixed morphological characters. In all of these examples, some traits may influence others in a unidirectional fashion, while other traits are mutually affected. Therefore, the most general and realistic description of interacting phenotypes includes the potential for multiple interactions and joint evolution of multiple traits. This can be accomplished with a multivariate model that allows for a combination of different interactions.

Taking the same approach as before, we define a vector of traits, \mathbf{z} , of an individual involved in an interaction

$$\mathbf{z} = \mathbf{a} + \mathbf{e} + \Psi\mathbf{z}' \quad (17)$$

Substituting for the vector of traits expressed by the partner in the interaction, \mathbf{z}' , we find

$$\mathbf{z} = (\mathbf{I} - \Psi\Psi)^{-1}(\mathbf{a} + \mathbf{e} + \Psi\mathbf{a}' + \Psi\mathbf{e}') \quad (18)$$

where \mathbf{I} is the identity matrix, \mathbf{a} is the vector of additive genetic effects, \mathbf{e} is the vector of environmental effects, and Ψ is the matrix of interaction effect coefficients (note that for combinations of traits that are not influenced by interactions, the corresponding elements of the Ψ matrix are zero). The mean values for the phenotypes are then described by

$$\bar{\mathbf{z}} = (\mathbf{I} - \Psi\Psi)^{-1}(\bar{\mathbf{a}} + \Psi\bar{\mathbf{a}}) \quad (19a)$$

or simply

$$\bar{\mathbf{z}} = (\mathbf{I} - \Psi)^{-1}(\bar{\mathbf{a}}) \quad (19b)$$

The vector of additive genetic effects, $\bar{\mathbf{a}}$, is a vector of direct genetic effects. The matrix $(\mathbf{I} - \Psi)^{-1}$ translates the direct genetic effects on traits into the indirect genetic effects on the traits they influence during interactions. That is, the $(\mathbf{I} - \Psi)^{-1}$ matrix accounts for all of the environmental influences caused by other traits during interactions; where elements of the Ψ matrix are zero, there are no environmental influences of other traits, and therefore no indirect genetic effects.

Multivariate phenotypic evolution is usually described by $\Delta\bar{\mathbf{z}} = \mathbf{C}_{az}\beta$, where \mathbf{C}_{az} is the covariance between additive genetic values and phenotypic values (cf. Arnold 1994). Se-

lection alters the phenotypic distribution and so $\mathbf{C}_{az}\beta$ predicts changes in the vector of additive genetic values (i.e., direct genetic contributions to the phenotype). For standard quantitative traits, the mean phenotype is described completely by the additive genetic value (Arnold 1994; Falconer and Mackay 1996), so $\mathbf{C}_{az}\beta$ adequately predicts the change in phenotype, $\Delta\bar{\mathbf{z}}$.

Because $\mathbf{C}_{az}\beta$ only predicts changes in the direct additive genetic contribution to traits, it is insufficient to describe changes in interacting phenotypes. That is why we considered the covariance between the breeding value and the phenotype in the univariate models of evolution presented above. However, to show how our model compares directly with standard multivariate models of evolution, we can consider evolution from the perspective reviewed by Arnold (1994).

Two complications arise when indirect genetic effects result from interactions. First, interactions alter the covariance between additive genetic values and phenotypes, because additive genetic values of other traits contribute to interacting phenotypes:

$$\mathbf{C}_{az} = \mathbf{G}(\mathbf{I} - \Psi^T\Psi)^{-1} \quad (20)$$

Second, the total change in an interacting phenotype must also include changes in traits that act as environmental influences, which are themselves predicted by $\mathbf{C}_{az}\beta$. Therefore, to predict total phenotypic change in interacting phenotypes, we must account for both changes in direct genetic contributions and indirect genetic contributions (i.e., environmental influences) to the phenotype. The pattern of indirect genetic effects is encompassed in the matrix $(\mathbf{I} - \Psi)^{-1}$, as seen in equation (18). The total phenotypic response to selection for interacting phenotypes is predicted by

$$\Delta\bar{\mathbf{z}} = (\mathbf{I} - \Psi)^{-1}(\mathbf{C}_{az}\beta) \quad (21)$$

Once again, we find that the rate of multivariate phenotypic change is profoundly altered by the presence of indirect genetic effects. The amount of change is directly proportional to the magnitude and sign of the elements of the interaction effect coefficient matrix, Ψ , that determines the strength of indirect genetic effects. Indirect genetic effects also alter the effect of selection on direct genetic effects, through their influence on phenotypes in the \mathbf{C}_{az} matrix.

DISCUSSION

In this work we reconcile the phenotypic expression of traits that are affected by social interactions (interacting phenotypes) and individual-based inheritance through a consideration of indirect genetic effects. Indirect genetic effects occur whenever genetic effects expressed in one individual influence the phenotype of a social partner, even when the individuals are unrelated. This view of inheritance alters our predictions about evolutionary change. Standard quantitative genetic models of phenotypic evolution (e.g., Lande 1979) assume a direct mapping of genotypes onto phenotypes. The existence of indirect genetic effects complicates this perspective and has non-intuitive evolutionary ramifications.

Interacting phenotypes differ from other traits because they are determined in part by an environment that can evolve, that is, traits of other individuals. The evolution of the en-

vironmental component is transmitted through the indirect genetic effects into phenotypic change in the focal trait. There are at least two evolutionary consequences of indirect genetic effects for all interacting phenotypes. First, the relative rate of phenotypic change is affected by the interaction. Second, variation in direct genetic effects (i.e., heritability) may not constrain phenotypic evolution.

These consequences can be illustrated by considering how direct and indirect genetic effects contribute separately to an evolutionary response to selection. To illustrate, we rearrange equation (8):

$$\Delta \bar{z}_1 = (G_{11}\beta_1 + G_{12}\beta_2) + \Psi_{12}(G_{12}\beta_1 + G_{22}\beta_2). \quad (22)$$

The first part of equation (22) now reflects the contribution of direct genetic effects and is the standard quantitative genetic equation for phenotypic change. The second part reflects the role of indirect genetic effects. Whenever there is an effect of the interaction (i.e., Ψ_{12} is non-zero), selection will result in additional phenotypic change in z_1 . Unlike standard quantitative genetic models, selection on z_1 (β_1) is also filtered through the genetic covariance between the two traits. Even more unexpected is that phenotypic change in z_1 can occur even when no genetic variation underlies that trait. This is because selection on z_2 , through the genetic variance for z_2 , results in a phenotypic change in z_1 when the interaction effect coefficient is non-zero. This non-intuitive result occurs because of the role of z_2 as an environmental effect.

Interactions have even more extreme effects on phenotypic evolution when there are reciprocal effects between traits. When two traits mutually influence each other, a feedback loop is generated, resulting in an additional term, $1/(1 - \Psi_{ij}\Psi_{ji})$, to the simple equation for evolutionary change. Whenever two traits influence each other in a similar way (either both positive or both negative), the response to selection is magnified because the denominator is less than one. Contrasting effects of interactions (one trait increases the expression of the other, but the reciprocal interaction decreases expression of the first trait) will slow down the rate of evolution. The magnitude of the effect of Ψ accelerates as Ψ approaches 1 or -1 (Fig. 3). In the multivariate case, these effects are contained in the $(\mathbf{I} - \Psi)^{-1}$ matrix.

Even when characters themselves are not involved in interactions, their evolution can be affected if there is a genetic covariance between the unaffected trait and an interacting phenotype expressed in interactions with reciprocal effects. For example, consider a character (e.g., a weapon) that itself is not directly affected by an interaction, but is genetically correlated to a trait that has a non-zero Ψ (e.g., aggression). Although direct responses to selection in the weapon are unaffected by the interaction because the weapon itself is unchanged by the interaction, the correlated response will still reflect the covariance between the breeding value of the weapon and the phenotype of aggression. Thus, the total evolutionary response of the weapon is

$$\Delta \bar{z}_2 = G_{22}\beta_2 + \left(\frac{G_{12}}{1 - \Psi_{11}^2} \right) \beta_1. \quad (23)$$

The indirect genetic effects that underlie the interacting phenotypes can have far-reaching effects, in this case magnifying the correlated response to selection of genetically correlated

traits. This effect will be seen whenever the interacting phenotype is reciprocally affected and a feedback loop is generated.

It is of interest to evaluate Ψ for a number of characters. Unfortunately, this is logistically difficult. The problem is analogous to determining breeding values for a trait; in fact, to determine Ψ one must hold the breeding value constant (analogous to estimating the maternal effect coefficient in maternal effect models, e.g., Kirkpatrick and Lande 1989). Most previous research on the genetics of social behavior has focused on holding the effects of the interaction constant to estimate the breeding value, for example testing individuals against a variety of inbred lines or tester stocks (see Fuller and Hahn 1976; Hahn and Schanz 1996). To evaluate Ψ , we can turn this around and evaluate how tester stocks or inbred lines vary in the phenotype that is expressed during interactions with different individuals. We can estimate Ψ as the slope $b_{z_i z_j}$, where z_i is the dependent phenotype of the focal individuals plotted against the independent phenotype of the tester individuals. If such stocks or lines are not available, we can hold breeding values constant by repeatedly testing the same individual against several other individuals. However, this approach invokes the assumption that experience has no effect on the phenotype that is expressed in successive interactions.

These considerations support the view of previous researchers who noted that evaluating quantitative genetic aspects of characters such as mating behavior, social dominance, aggression, or other characters expressed only during interactions is difficult and potentially misleading if standard breeding designs are used (Fuller and Hahn 1976; Boake 1989, 1994; Hahn and Schanz 1996). Testing against inbred lines, isofemale strains, or tester stocks can circumvent potentially inflated estimates of genetic variance. Artificial selection provides an additional empirical tool for evaluating how traits expressed during interactions might change. Neither approach can be used to estimate realized heritabilities because the effect of Ψ remains unmeasured.

Finally, although we have assumed that the interaction effect coefficient is a fixed value in these models, it seems likely that Ψ itself can evolve. Behavioral ecologists have explored the fitness consequences of different strategies of behavioral response through a game theory approach (Maynard Smith 1982; Grafen 1991). Our interaction effect coefficient, Ψ , can be viewed as a parameter describing this response strategy; to the extent that Ψ is a variable, genetically-based character of individuals it may respond evolutionarily to such selection pressures. Our preliminary investigations further suggest that the evolution of Ψ can lead to phenotypic integration among traits without underlying genetic covariances.

Although no studies have evaluated all of the parameters of our model, there is empirical support for the notion that traits expressed during interactions may evolve differently than other characters and depend on genetic differences among social partners. A recent study by Rice (1996) suggests that preventing the evolution of the indirect genetic component can change the evolution of intersexual interactions in *Drosophila*. Hughes (1989) found that levels of exploratory and agonistic behavior of mice depend on the social

composition of genotypes (i.e., the genetic architecture of the social group). Male courtship in *Drosophila* is dependent, at least in part, on the genotype of the interacting female (Casares et al. 1993). Artificial selection studies support the idea that territoriality (Hoffmann 1994), mating behavior (Manning 1961, 1963; Welbergen and van Dijken 1992), aggression (Guhl et al. 1960; Bakker 1986; Hemmat and Eggleston 1988), communication (Ritchie and Gleason 1995), and social dominance (Craig et al. 1965; Francis 1984; Dewsbury 1990; Moore 1990) can evolve relatively faster than other traits.

Previous considerations of the evolution of interacting phenotypes have concentrated on the differences in selection rather than inheritance (West-Eberhard 1979, 1983, 1984; Wade 1980, 1985; Lande 1981; Quellar 1992a,b; Tanaka 1991, 1996) or on maternal effects (Mousseau and Fox, in press). While many of these studies of selection have noted the potential for relatively faster evolution of interacting phenotypes, these models have considered only simple inheritance. Our model offers a quantitative genetic framework for understanding the complex inheritance generated during interactions. The combination of previous considerations of selection resulting from interactions with our model of inheritance of interacting phenotypes suggests that the rate of evolution for such traits may be even more rapid than previously appreciated. We now need empirical studies that evaluate the extent and role of interactions in phenotypic evolution given the perspective we have presented here.

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APPENDIX

Phenotypic Variances

The phenotypic variance of traits with a phenotype defined by equations (17) and (18) can be derived in two forms. The first we present is simpler but is circular in its definition. The second is more complex but has the preferred characteristic of being noncircular.

An equation where \mathbf{P} is defined by several terms including \mathbf{P} itself can be derived:

$$\mathbf{P} = \text{Cov}[\mathbf{z}, \mathbf{z}^T]. \quad (\text{A1})$$

where the superscript T denotes matrix transposition. By expanding and substituting, using equation (17) to define the vector of phenotypes of interest,

$$\mathbf{P} = \text{Cov}[\mathbf{a} + \mathbf{e} + \Psi\mathbf{a}' + \Psi\mathbf{e}' + \Psi\Psi\mathbf{z}, \mathbf{z}^T]. \quad (\text{A2})$$

Taking the covariance:

$$\mathbf{P} = \mathbf{C}_{\mathbf{a}\mathbf{z}} + \mathbf{C}_{\mathbf{e}\mathbf{z}} + \text{Cov}(\Psi\mathbf{a}', \mathbf{z}^T) + \text{Cov}(\Psi\mathbf{e}', \mathbf{z}^T) + \Psi\Psi\mathbf{P} \quad (\text{A3})$$

where $\mathbf{C}_{\mathbf{a}\mathbf{z}} = \text{Cov}(\mathbf{a}, \mathbf{z}^T)$ and $\mathbf{C}_{\mathbf{e}\mathbf{z}} = \text{Cov}(\mathbf{e}, \mathbf{z}^T)$. Because the phenotype of the other individual influences the expression of \mathbf{z} , the term $\text{Cov}[\Psi\mathbf{a}', \mathbf{z}^T]$ reduces to $\text{Cov}[\Psi\mathbf{a}', \Psi\mathbf{z}^T]$ and $\text{Cov}[\Psi\mathbf{e}', \mathbf{z}^T]$ reduces to $\text{Cov}[\Psi\mathbf{e}', \Psi\mathbf{z}^T]$. Taking these covariances and collecting terms, we get

$$\mathbf{P} = \mathbf{C}_{\mathbf{a}\mathbf{z}} + \mathbf{C}_{\mathbf{e}\mathbf{z}} + \Psi\mathbf{C}_{\mathbf{a}\mathbf{z}}\Psi^T + \Psi\mathbf{C}_{\mathbf{e}\mathbf{z}}\Psi^T + \Psi\Psi\mathbf{P} \quad (\text{A4})$$

Using this equation one can easily solve for values of \mathbf{P} , although not directly.

We can solve for an alternative definition of the phenotypic variance that allows us to solve directly for any value of \mathbf{P} . Substituting equation (18) for \mathbf{z} and \mathbf{z}^T in (A1) we get:

$$\mathbf{P} = \text{Cov}[(\mathbf{I} - \Psi\Psi)^{-1}[\mathbf{a} + \mathbf{e} + \Psi\mathbf{a}' + \Psi\mathbf{e}']],$$

$$[(\mathbf{I} - \Psi\Psi)^{-1}[\mathbf{a} + \mathbf{e} + \Psi\mathbf{a}' + \Psi\mathbf{e}']]^T \quad (\text{A5})$$

Again, collecting terms and assuming the interacting individuals are unrelated,

$$\mathbf{P} = (\mathbf{I} - \Psi\Psi)^{-1} (\mathbf{G} + \mathbf{E} + \Psi\mathbf{G}\Psi^T + \Psi\mathbf{E}\Psi^T)(\mathbf{I} - \Psi^T\Psi^T)^{-1}. \quad (\text{A6})$$

From these general equations we can derive the expected phenotypic variances and covariances for the three examples in the text. As an illustration, the following are the phenotypic variances

and covariances where there are reciprocal effects of interactions involving two different traits. In this case the Ψ matrix has the form

$$\Psi = \begin{bmatrix} 0 & \Psi_{12} \\ \Psi_{21} & 0 \end{bmatrix} \quad (\text{A7})$$

and therefore, using equation (A6), the phenotypic variances and covariances are defined as

$$P_{11} = \frac{1}{(1 - \Psi_{12}\Psi_{21})^2} (G_{11} + E_{11} + \Psi_{12}^2 G_{22} + \Psi_{12}^2 E_{22}), \quad (\text{A8a})$$

$$P_{22} = \frac{1}{(1 - \Psi_{12}\Psi_{21})^2} (G_{22} + E_{22} + \Psi_{21}^2 G_{11} + \Psi_{21}^2 E_{11}), \quad (\text{A8b})$$

$$P_{12} = P_{21} = \frac{1}{(1 - \Psi_{12}\Psi_{21})^2} (G_{21} + E_{21} + \Psi_{21}\Psi_{12}G_{12}). \quad (\text{A8c})$$