Social Effects

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Glossary

Altruism Any behavior that benefits a conspecific at a cost to the actor's own fitness.
Hamilton's rule A rule first derived by William Hamilton predicting that altruism should be favored by selection when fitness costs are outweighed by benefits to related individuals.
Indirect genetic effect The influence of the genes of one individual on the phenotypic expression of another.
Nonsocial selection The influence of an individual's phenotype on its own fitness.
Social selection The influence of the phenotype of one individual on the fitness of another.

Social interactions among conspecifics are ubiquitous in nature (Frank, 2007). Some species, such as the eusocial insects (ants, bees, wasps, and termites), form complex societies with differentiated castes and division of labor (Wilson, 1971). In these species, social interactions are obviously important for fitness. For example, a queen bee would be unable to reproduce without the cooperation of workers who forage and provide parental care for the colony. In other species, the importance of social interactions might be less obvious but no less important. For example, social competition among conspecifics for resources or mates is often both highly important for fitness and reliant on social interactions (West-Eberhard, 1979). Quorum sensing in bacteria, reproductive aggregation in slime molds, and chemical communication in plants serve as reminders that the importance of social interaction is not limited to animals but extends across all of life's kingdoms (West *et al.*, 2006; Frank, 2007; Karban, 2008).

Despite their importance in nature, social interactions were mostly ignored by evolutionary biologists for over 100 years after the publication of the *Origin of Species*. The founders of theoretical population genetics, Haldane, Fisher, and Wright, made occasional references to sociality but were largely concerned with other issues. A major breakthrough came in 1964 with the publication of Hamilton's theory of inclusive fitness, which demonstrated the evolutionary consequences of genes that influence the fitness of related individuals (Hamilton, 1964a,b). Specifically, Hamilton showed that alleles associated with altruistic behavior may evolve by natural selection when the cost to the actor's fitness is outweighed by benefits to relatives. This prediction has become known as Hamilton's rule.

Later in the decade, Griffing began to explore the consequences of what he called 'associate effects,' which occur when the genes of one individual affect the phenotype of another (Griffing, 1967). Griffing's contribution has received much less attention than Hamilton's, but as will be shown below, such associate effects (or indirect genetic effects (IGEs), as they are typically called today) may have major implications for the evolution of social phenotypes. Today, the work of Hamilton and Griffing has been integrated into the standard quantitative genetic model of evolution, allowing specific predictions for social phenotypes should evolve (Queller, 1992a,b; Moore *et al.*, 1997; Wolf *et al.*, 1999; Bijma *et al.*, 2007; Bijma and Wade, 2008; McGlothlin *et al.*, 2010, 2014). What follows is a brief overview of relevant theory and empirical approaches that explore how social interactions affect the evolutionary process.

Theoretical Background

Two necessary conditions must be met for a trait to evolve by natural selection. First, the trait must be predictably associated with fitness; that is, it must be under natural selection. Second, the trait must exhibit genetic variation such that offspring tend to resemble their parents. To show how these two conditions contribute to adaptive evolution, biologists tend to use the quantitative genetic model of phenotypic evolution, which shows that under many conditions, phenotypic evolution can be predicted by the breeder's equation:

$$\Delta\bar{z} = G\beta$$

(Lande, 1979; Lande and Arnold, 1983; Falconer and MacKay, 1996). This simple equation shows that evolutionary change in the population mean of a trait ($\Delta\bar{z}$) can be predicted by the product of additive genetic variance (G), a measure of the similarity between parents and offspring, and the selection gradient (β), which measures the slope of the relationship between a trait and fitness. Both G and β can be estimated empirically, making this model a powerful way to study evolution in natural populations (Endler, 1986; Mousseau and Roff, 1987, 1997; Kingsolver *et al.*, 2001).

Social interactions among individuals can lead to complexities that alter the predictions of the breeder's equation. Specifically, social interactions can lead to violation of two important assumptions: that traits can be neatly decomposed into genetic and environmental components and that an individual's fitness can be attributed primarily to an individual's own traits. Violation of these two assumptions lead to two pathways by which social interactions can affect evolutionary change: by altering the phenotypes of interacting individuals, giving rise to IGEs, and by directly influencing fitness, giving rise to social selection (**Figure 1**).

Indirect Genetic Effects

The simplest quantitative genetic model assumes that the expression of a trait, z, can be attributed to two sources: an additive genetic component, a, which contributes to the

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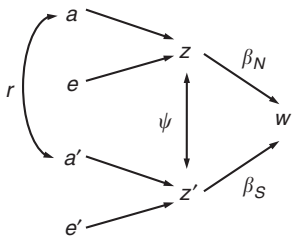

Figure 1 Pathways by which social interactions may influence evolutionary response to selection. In the absence of social interactions, an individual's fitness (w) is influenced only by its own traits (z), which are a function of its genes (a) and environment (e). The strength of this relationship is known as nonsocial selection (β_N). Social interactions may alter this pathway in two ways. First, an individual's phenotype may be influenced by the phenotypes of another individual (z') with strength ψ, leading to indirect genetic effects (IGEs). Because such interactions can involve feedback, this effect is shown as a double-headed arrow. Second, the social partner's phenotype may directly influence fitness, leading to social selection (β_S). Social selection can alter evolutionary response in the presence of IGEs, relatedness (r), or both.

similarity of parent and offspring traits, and an environmental component, e. To obtain an individual's phenotypic value, these components are simply added together:

$$z = a + e$$

Now consider a trait whose expression depends upon a trait in another individual. Animal behavior provides numerous examples of such traits. For example, a territorial holder's aggressive response might depend on the body size of the invader it encounters. These effects can also arise via feedback between the same phenotype expressed in different individuals. For example, a bird might sing more intensely when it hears song from another bird. At the same time, the second bird may be adjusting its song in response to the first. Although these effects on phenotypic expression may seem like just another part of the environment, they may alter evolutionary predictions because now the environment depends upon the traits of others and thus has a genetic component of its own.

The dependence of an individual's phenotype on genes found in another individual is known as an IGE. (Most of the treatment below follows the model of Moore *et al.* (1997), which introduced this term.) Such effects can be modeled by introducing another term into our phenotypic equation:

$$z_i = a_i + e_i + \psi_{ij} z'_j$$

The new term $\psi_{ij} z'_j$ represents the effect of a second individual's trait (z'_j) on the expression of the first individual's trait (z_i). The subscripts i and j allow the consideration of both cases sketched above, and the prime on the latter trait is used to indicate that the trait belongs to a second individual. When i and j are different, this equation represents cases like the adjustment of aggression based on invader body size; when i and j are the same, it represents cases of feedback, like the birdsong example. The coefficient ψ_{ij} represents the strength and direction of the interaction. If ψ_{ij} is positive, z_i increases in response to larger values of z'_j, whereas if ψ_{ij} is negative, the opposite occurs.

IGEs arise when the trait of the interacting individual is heritable. In this case, z'_j can be broken down into an additive genetic effect and an environmental effect of its own:

$$z_i = a_i + e_i + \psi_{ij}(a'_j + e'_j)$$

It is clear from this equation that the expression – and hence the evolution – of trait z_i will depend on both a direct genetic effect or DGE (a_i), which is attributable to an individual's own genes, and an IGE ($\psi_{ij} a'_j$), which is attributable to genes of its social partner. (Again, the primes denote that values belong to a second individual.) Even more complexity can arise when feedback is incorporated into the model. This may occur when one trait influences the same trait in another individual, as in the birdsong example, or when two traits influence each other in a loop. For example, animals might have both aggressive and submissive displays that they may use in an agonistic encounter. The aggressive display from one individual might elicit the submissive display from the other, and in turn, the submissive display might suppress the aggressive display. Such loops can be modeled by adding another term:

$$z_i = a_i + e_i + \psi_{ij}(a'_j + e'_j + \psi_{ji} z_i)$$

After some algebra, this can be written as

$$z_i = \frac{a_i + e_i + \psi_{ij}(a'_j + e'_j)}{1 - \psi_{ij}\psi_{ji}}$$

The denominator of this equation shows that feedback loops will influence the magnitude of both DGEs and IGEs. This effect will depend on the signs of the two ψ coefficients.

These social effects on the expression of phenotypes lead to alterations in the predictions of the breeder's equation. Consider the case of a phenotype that triggers a change in the same phenotype in an unrelated individual, like the birdsong example above. In this case, the predicted change in response to selection is

$$\Delta\bar{z} = \frac{G\beta}{(1-\psi)(1-\psi^2)}$$

The subscripts have been dropped here because this equation considers only a single trait. This equation shows that when a single trait is considered, IGEs affect evolutionary predictions in two ways. First, the term $(1-\psi)$ in the denominator shows that the simple presence of IGEs increases the response to selection when ψ is positive and decreases it when ψ is negative. This effect arises because the genes an individual passes on to its offspring will influence both their own phenotype and the phenotypes of others. When social interactions cause individuals to express more similar phenotypes, effective genetic variance (and thus response to selection) is increased. Social interactions that cause individuals to become more different from each other have the opposite effect.

Second, the term $(1-\psi^2)$ in the denominator arises from feedback in social interactions. Feedback is more important for very strong values of ψ, and cause a rapidly increasing response to selection as ψ becomes more positive. When ψ is negative,

feedback effects can overwhelm the depressive effect of IGEs on genetic variance, leading to a very strong response to selection for values of ψ around -0.9 and smaller. It is unknown whether such values are likely to be realistic, however. As will be discussed later, empirical estimates of ψ are limited, but there is currently no evidence for extreme negative values of ψ.

IGEs may also influence how responses to selection on multiple traits. In the absence of IGEs, a trait may evolve in response to selection on a second trait if the two traits are genetically correlated:

$$\Delta\bar{z}_1 = G_{11}\beta_1 + G_{12}\beta_2$$

In this equation, G_{11} refers to the additive genetic variance in trait z_1 and G_{12} is the additive genetic covariance between the two traits. Clearly, z_1 may evolve even when selection does not act directly on it (i.e., $\beta_1=0$) if z_2 is under selection ($\beta_2 \neq 0$) and the two traits covary genetically ($G_{12} \neq 0$). IGEs may alter this prediction by creating genetic relationships between traits that are otherwise uncorrelated. Consider the case when z_1 is influenced by z_2' in unrelated social partners ($\psi_{12} \neq 0$). If these two traits show no additive genetic correlation ($G_{12} \neq 0$), such IGEs can still cause the evolution of the two traits to be intertwined:

$$\Delta\bar{z}_1 = G_{11}\beta_1 + \psi_{12}G_{22}\beta_2$$

Note that the social effect causes z_1 to evolve in response to selection on z_2 even though the two traits are genetically uncorrelated. The quantity $\psi_{12}G_{22}$, which is the IGE coefficient multiplied by the genetic variance in trait 2, plays the same role as the additive genetic covariance G_{12} above. Interestingly, this equation also shows that z_1 may evolve in response to selection on z_2 even when it shows no additive genetic variance of its own ($G_{11}=0$). This would not be true in the absence of IGEs because genetic covariance is by definition absent when genetic variance is absent.

Social Selection

The second pathway by which social interactions may influence the evolutionary process is via direct effects on fitness. The effect of the phenotype of one individual on the fitness of another is known as social selection (Wolf *et al.*, 1999). Social selection may arise whenever social interactions have fitness consequences that depend on phenotype. For example, if agonistic encounters when larger individuals tend to inflict more harm, social selection would be acting through body size.

Like ordinary natural selection, or 'nonsocial' selection, social selection will only lead to evolutionary change under certain conditions. For nonsocial selection, the relevant variable is genetic variance, but what matters for social selection is the correlation between interacting individuals. Specifically, social selection will only lead to an evolutionary change when there is a nonrandom association between an individual's genes and the phenotype of its social partner (McGlothlin *et al.*, 2010). Using the example above, if large individuals inflicted harm and also sought out smaller individuals to bully, social selection would lead to an evolutionary increase in body size. It is easy to see why this is true: small individuals suffer the most from aggression and thus have the lowest fitness.

To add social selection to an evolutionary model, fitness must be divided into two components: one deriving from an individual's own traits and one deriving from those of social interactants. The simplest version of such a model considers the same trait in two socially interacting individuals. In this model, an equation for relative fitness can be written as

$$w = \alpha + \beta_N z + \beta_S z' + \varepsilon$$

where w is relative fitness, β_N is the nonsocial selection gradient, β_S is the social selection gradient, and α and ε are an intercept and an error term, respectively (Wolf *et al.*, 1999). Although social selection can involve any phenotype, it is easiest to envision acting through behavioral traits: β_S should be positive for behaviors that tend to help another individual (cooperation or altruism) and negative for behaviors that harm another individual (such as physical aggression).

As mentioned above, an evolutionary response to social selection depends on an association between one individual's genes and another's phenotype. This relationship can arise in two different ways: either individuals nonrandomly interact with one another, or IGEs may alter the expression of phenotypes during interactions. As noted above, IGEs are quantified with the parameter ψ. To model nonrandom association, the parameter r is used. This parameter is usually called relatedness, because one of the easiest ways to get a nonrandom phenotypic association is for relatives to interact. However, familial relatedness is not necessary; any nonrandom assortment (such as big individuals seeking out smaller individuals) will do.

Adding these effects to the breeder's equation yields:

$$\Delta\bar{z} = \frac{(1 + r\psi)G\beta_N + (r + \psi)G\beta_S}{(1 - \psi)(1 - \psi^2)}$$

This equation shows that evolutionary response to social selection depends on the quantity $(r+\psi)$, that is, on the presence of relatedness, IGEs, or both (McGlothlin *et al.*, 2010). In addition, the response to nonsocial selection is altered somewhat when both relatedness and IGEs are present $(1+r\psi)$. Social selection can either act in opposition to or in concert with nonsocial selection. The former case is the most interesting, because here the levels of selection are in conflict; in other words, different trait values are favored when we consider an individual's fitness versus the fitness of others. When levels of selection are in conflict, the evolutionary outcome will reflect a balance between nonsocial and social selection. This balance will be determined both by the strength of each selection gradient and the combined effect of relatedness and IGEs.

The most instructive case to examine here is the same one that concerned Hamilton: the evolution of altruism. Altruism occurs when others are helped at the expense of one's own fitness, and hence altruistic behaviors should have positive β_S (Hamilton's 'benefit') and negative β_N (Hamilton's 'cost'). Thus, an altruistic behavior should increase in response to selection ($\Delta\bar{z}>0$) when:

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

This inequality, which is a slight modification of Hamilton's rule, demonstrates that relatedness and reciprocity can have symmetrical and complementary effects on the evolution of altruism (McGlothlin *et al.*, 2010). In words, this inequality shows that altruism should increase in a population when fitness costs to oneself are outweighed by scaled benefits to others. As Hamilton identified, the effective benefit increases with relatedness; for example, altruistic behavior is more likely to evolve when full-sibs ($r=0.5$) benefit than when half-sibs ($r=0.25$) benefit. Similarly, IGEs enhance the evolution of altruism when ψ is positive, leading interacting individuals to be more similar to each other and slow its evolution when ψ is negative. Positive values of ψ can favor the evolution of reciprocal altruism, a form of cooperation where one individual's actions depend on the actions of its social partner. The modified form of Hamilton's rule indicates that this type of reciprocity can lead to the evolution of cooperation among unrelated individuals ($r=0$) when ψ is strong enough. When both factors are present, they can interact to influence the evolution of altruism.

Empirical Examples

The power of the framework outlined above is that relevant parameters can be estimated in natural populations, allowing evolutionary biologists to assess the importance of social interactions in the evolutionary process. The study of social interactions has traditionally been the domain of behavioral ecology, and its synthesis with evolutionary quantitative genetics is still in its infancy. Empirical work at the nexus of these two fields has begun to bear fruit in recent decades. This section will briefly explore empirical studies of IGEs and social selection and their relevance to understanding evolution interacting phenotypes.

Indirect Genetic Effects

IGEs can be studied empirically taking one of two approaches. Trait-based approaches follow directly from the theory outlined above and attempt to assess the importance of particular phenotypes in generating IGEs (McGlothlin and Brodie, 2009). In contrast, variance-partitioning approaches assess the total strength of IGEs on a particular phenotype without assigning these effects to a particular phenotype in an interacting individual (Wolf, 2003; Muir, 2005; Bijma *et al.*, 2007; Bijma, 2010). Each of these approaches has its advantages and disadvantages, and the choice depends upon the question being asked. Fortunately, the two frameworks are compatible in theory, and results from one framework may often be translated to the other (McGlothlin and Brodie, 2009; McGlothlin *et al.*, 2010).

Studies that measure IGEs use simple modifications of methods used to detect standard quantitative genetic parameters such as heritability. Two ingredients are of prime importance for such studies. First, as for any quantitative study, the investigator must have knowledge of the genetic relatedness among the individuals under study. This is often accomplished using a controlled breeding design, such as mating males to multiple females to generate half-sib families, but may also involve complex natural pedigrees or experimentally generated inbred lines (Falconer and MacKay, 1996). Second, associations among individuals must be known in order to quantify the effects of social interactions (Muir, 2005; Bijma *et al.*, 2007). This may derive from housing individuals together in a laboratory environment or observing natural social groups in the wild.

Most empirical studies of IGEs have used a variance-partitioning approach, and the bulk of this work has been conducted in domestic species such as laying hens or hogs (Bijma *et al.*, 2007; Ellen *et al.*, 2008; Wade *et al.*, 2010). One particularly nice example comes from a study of mortality in domestic fowl (Bijma *et al.*, 2007). Group-housed hens suffer socially induced mortality due to cannibalistic pecking. A large study of 4000 hens with a known pedigree showed that nearly two-thirds of the genetic variation in survival derived from IGEs rather than DGEs. There was no strong correlation between direct and indirect effects, suggesting that avoidance of pecking and pecking others are genetically independent.

Some work has been conducted in nondomestic species as well. In one study that quantified IGEs in aggressive interactions between male deer mice (*Peromyscus maniculatus*) in the laboratory, Wilson *et al.* (2009) detected evidence for IGEs in three of the five traits they measured. Notably, all three traits showed strong correlations between direct and indirect effects. Dominant individuals tend to mount subordinates, and the rate of mounting showed a strong negative correlation between direct and indirect effects. This relationship likely indicates a negative value of ψ: individuals that tend to be submissive induce dominant behavior in their partners and vice versa. This is predicted to lead to a slower response to selection than would occur in the absence of IGEs (cf. Wolf, 2003). Two other traits, rearing (a threat display) and time to initiate a fight, showed strong positive direct–indirect correlations, indicating the presence of positive values of ψ. This result suggests that IGEs should cause certain aggressive behaviors to respond very rapidly to selection.

Although the analyses presented by Wilson *et al.* (2009) suggest certain values of ψ, they cannot directly estimate it because they do not use a multivariate approach to tease apart relationships among correlated traits. Only a few studies have attempted to estimate ψ directly. In one pioneering study, Bleakley and Brodie (2009) used a clever experimental design to estimate ψ for predator inspection behaviors in guppies. This study took advantage of the many available designer guppy strains, which are similar to inbred lines, allowing the experimenters to control the genetic makeup of social groups. Several different strains were placed in groups with a focal individual, and the regression of focal on social group behaviors provided estimates of ψ. Significant estimates of ψ were overwhelmingly positive and tended to involve the same behavior in focal and social individuals. This suggests a pattern of reciprocity: guppies are more likely to approach a predator or school if others do as well. This positive feedback should allow these behaviors to respond rapidly to selection.

In certain systems, direct and IGEs may be assigned to particular regions of the chromosome, sometimes even to particular genes. For example, Mutic and Wolf (2007) used inbred lines of the plant *Arabidopsis thaliana* to map

quantitative-trait loci underlying direct and indirect effects on a number of traits related to plant size and development. Interestingly, direct and indirect effects of given loci tended to be of the same sign, suggesting a pattern of cooperation rather than competition among plants.

Social Selection

Studies that estimate natural selection in wild populations tend to use a regression-based method that teases apart the direct effects of correlated traits on fitness. The partial regression slopes generated by these analyses provide estimates of selection gradients, i.e., a measurement of direct natural selection on each trait (Lande and Arnold, 1983). Social selection can be measured in natural populations using a simple modification such analyses (Heisler and Damuth, 1987; Goodnight *et al.*, 1992; Wolf *et al.*, 1999). In addition to including an individual's own traits as predictors of fitness, a social selection analysis would include phenotypic values from one or more social interactants. The partial regression slopes for an indivdual's own traits would estimate nonsocial selection gradients (β_N), while the slopes for the traits of social interactants would estimate social selection (β_S).

Studies directly applying social selection analysis in wild populations are very rare. One example of social selection comes from a study of forked fungus beetles, which live in groups on bracket fungi (Formica *et al.*, 2011). Social interactions among males are often aggressive and involve competition over access to mates, and larger males typically have the advantage in such contests. Formica *et al.* (2011) found that mating success, which was estimated by observing copulations, was predicted not only by a male's own size but also that of the males with which he interacted. Specifically, males with the highest mating success were larger (positive β_N) and surrounded by smaller competitors (negative β_S). Such social selection is probably common in the context of sexual selection, where a male's trait relative to local competitors is likely to be more important than his absolute trait value. Interestingly, Formica *et al.* found that larger males tended to be surrounded by smaller males. Although they did not measure genetic relationships among individuals, this phenotypic correlation suggests the possibility of a nonrandom genetic association between interacting males, which would predict an evolutionary response to social selection.

Conclusion

Theory shows that when social interactions affect phenotypes, fitness, or both, evolutionary responses to selection may be drastically altered. Depending on the nature of the interaction, evolutionary change may be accelerated or slowed. In addition, traits that are not otherwise genetically correlated may coevolve via their roles in social interactions. The effects of social interactions on evolutionary change may be probed empirically using subtle tweaks of standard quantitative genetic methods. Although early work has provided foundational evidence that IGEs and social selection may be important in nature, the field is still in its infancy and much more work is necessary to establish the evolutionary roles played by these phenomena.

See also: Genotype-by-Environment Interaction. Natural Selection, Measuring

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