



Symposium Article

Phenotypic Assortment Changes the Landscape of Selection

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Abstract

Social interactions with conspecifics can dramatically affect an individual's fitness. The positive or negative consequences of interacting with social partners typically depend on the value of traits that they express. These pathways of social selection connect the traits and genes expressed in some individuals to the fitness realized by others, thereby altering the total phenotypic selection on and evolutionary response of traits across the multivariate phenotype. The downstream effects of social selection are mediated by the patterns of phenotypic assortment between focal individuals and their social partners (the interactant covariance, C^{ij} , or the multivariate form, C). Depending on the sign and magnitude of the interactant covariance, the direction of social selection can be reinforced, reversed, or erased. We report estimates of C^{ij} from a variety of studies of forked fungus beetles to address the largely unexplored questions of consistency and plasticity of phenotypic assortment in natural populations. We found that phenotypic assortment of male beetles based on body size or horn length was highly variable among subpopulations, but that those differences also were broadly consistent from year to year. At the same time, the strength and direction of C^{ij} changed quickly in response to experimental changes in resource distribution and social properties of populations. Generally, interactant covariances were more negative in contexts in which the number of social interactions was greater in both field and experimental situations. These results suggest that patterns of phenotypic assortment could be important contributors to variability in multilevel selection through their mediation of social selection gradients.

Keywords: beetle, indirect genetic effects, kin selection, social behavior, social network, social selection

All organisms live within a social context comprised of the identities and features of conspecifics (Frank 2007). This fact seems obvious for the species we often think of as social—eusocial insects and mammals, colonial invertebrates and vertebrates, animals that live together in groups of related individuals at some life stage—but it applies universally even to taxa that do not clearly live in group settings. Territorial individuals have neighbors, sexual species must seek out and interact with mates, and sessile taxa like plants or corals experience and often compete with neighbors. All of these kinds of

interactions generate opportunities for social contexts, which are environments that contain genes, to generate causal and correlative impacts on evolution.

There are 3 distinct pathways through which social contexts alter the evolutionary process from the traditional conceptualization of individual-centric inheritance and selection. First, there are general fitness effects. The mere act of being in a group or engaging with conspecifics may increase (e.g., through group defense or foraging) or decrease (e.g., through higher disease transmission or competition) fitness for

group members (Alexander 1974; Brown and Brown 1996; Krause and Ruxton 2002). Other fitness consequences depend on the traits of group members (e.g., costs of competing with larger partners), which are usually described through the social selection gradient, β_S (Figure 1) (Frank 1997; Wolf et al. 1998, 1999; McGlothlin et al. 2010).

The second way in which social partners alter the evolutionary process is by changing how conspecifics express their own phenotypes. When traits are plastic and respond to variation in the traits of conspecifics, a causal link results between traits in one individual and traits in another (Moore et al. 1997; Wolf et al. 1998). The direct phenotypic effect of one individual's trait (z'_j) on a conspecific's (z_i) is quantified as the interaction coefficient, ψ . This effect is directional and can include effects of the same trait (ψ_{ii}), or different traits (ψ_{ij}) in social partners (usually denoted by a prime) (Figure 1). At the population level, phenotypic variation in one trait becomes linked to another, creating feedback loops in which genetic variation for one character can be the source of evolutionary response in another (Griffing 1977; Kirkpatrick and Lande 1989; Moore et al. 1997; Wolf et al. 1998; McGlothlin et al. 2010).

The third evolutionary impact of social context, and the one we focus on in this article, is that it can change the targets, strength, and directions of phenotypic selection. When social partners impact fitness, such as when larger competitors win battles over resources, or mates provide direct benefits to partners, those negative or positive consequences are only experienced by their partners and not the general population. The resultant effects on phenotypic selection emerge at the population level whenever social selection gradients are experienced nonrandomly among individuals (Queller 1992a, 1992b; Wolf et al. 1999; McGlothlin et al. 2010; Formica et al. 2011a). In other words, the traits in social partners that explain variance in the fitness of focals are correlated with some trait in those same focals. Here we explore how these phenotypic correlations among social partners generates indirect selection and can alter the total selection differential that impacts a trait. The correlation that determines net selection is between traits in different individuals, not within the same individual (Figure 2). This phenotypic assortment is measured as the covariance of interactants (or "interactant covariance"), C^{ij} , where z_i is a trait in a focal individual and z'_j is a trait in the social context (denoted with a prime) (Wolf et al. 1999; Formica et al. 2011a; McDonald et al. 2017). The trait z'_j could be a character in single partner in a dyadic interaction, or the average of values of the members of a social group, or some function weighted by the symmetrical interactions experienced across a complex social

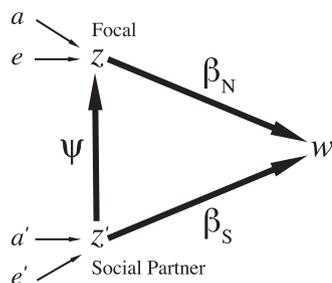


Figure 1. Interacting phenotypes between social partners. The phenotype of a focal individual z influences its own fitness through the nonsocial selection gradient, β_N . The phenotype of a social partner (or group of social partners, denoted with a prime), z' , affects the focal individual's fitness through the social selection gradient, β_S . Social partners can also influence the phenotype of focal individuals through the interaction coefficient, ψ . Additive genetic, a , and environmental, e , influences on phenotypes are also shown for both focal and social partner traits.

network (Figure 2). Often, we are interested in the correlations among partners with respect to the same trait, z_i , in both focals and partners, C^{ij} . The interactant covariance is simply a measure of association and does not imply causal effects of one trait on another.

Pathways of Social Selection

To trace how this interactant covariance, C^{ij} , can alter patterns of phenotypic selection, we identify it in a multivariate selection path framework used to distinguish direct and indirect pathways to fitness (Figure 3). In the usual application of this model, individuals have multiple traits (z_1, z_2, \dots, z_n) any of which can affect variance in fitness (Arnold 1983, 2003). The paths that lead from trait values to fitness are phenotypic selection gradients measured as partial regression coefficients that identify the effect of one trait, independent of variance in all the other traits in the model. Phenotypic correlations within individuals are represented by double-headed arrows among traits. The well-known result of this kind of path model approach is that phenotypic traits often experience indirect selection through correlated traits that influence fitness (Lande and Arnold 1983; Brodie et al. 1995). The strength of this indirect selection path is the product of the phenotypic covariance and the selection gradient on the correlated traits.

Social selection enters the path framework in much the same way, except that the traits of interest are not expressed in the same individual, but instead in the social partners with which the focal interacts (Queller 1992b; Frank 1997; Wolf et al. 1999). If those social context traits explain variance in fitness, there is a nonzero social selection gradient, β_S . Each social-trait-specific gradient (β_{S_i}) generates net indirect selection on focal phenotypes if and only if there is phenotypic assortment between focal and social traits that generates a nonzero C^{ij} . From the perspective of any single trait in the focal, the total selection (s_i) experienced by a trait z_i is a combination of direct nonsocial selection (β_{N_i}), indirect nonsocial selection (β_{N_j}), and indirect social selection β_{S_i} and β_{S_j} , summed up for 2 traits z_i and z_j as

$$s_i = Cov(z_i, z_j) \beta_{N_j} + Cov(z_i, z'_j) \beta_{S_j} \quad (1)$$

or expanded

$$s_i = Var(z_i) \beta_{N_i} + Cov(z_i, z_j) \beta_{N_j} + Cov(z_i, z'_j) \beta_{S_j} + Cov(z_i, z') \beta_{S_i} \quad (2)$$

In both equations, the β_N terms describe direct and indirect selection in the traditional sense, wherein selection relates individual phenotypes to fitness. The β_S terms describe the indirect effects of social selection due to fitness effects of the phenotypes of social partners. In multivariate terms, the selection differential can be generalized as

$$S = P \beta_N + C^I \beta_S \quad (3)$$

where P is the phenotypic-variance covariance matrix within individuals and C^I is the matrix of the covariance of interactants among individuals (or focals and social contexts).

These equations describe only the within-generation forces of phenotypic selection. This selection is translated into evolutionary response across generations through patterns of multivariate inheritance, which can be further complicated by interacting phenotypes (McGlothlin et al. 2010).

These simplified formulations assume that both nonsocial and social selection are linear and univariate. Some of the more interesting cases of social interaction, especially those involving behavior, might

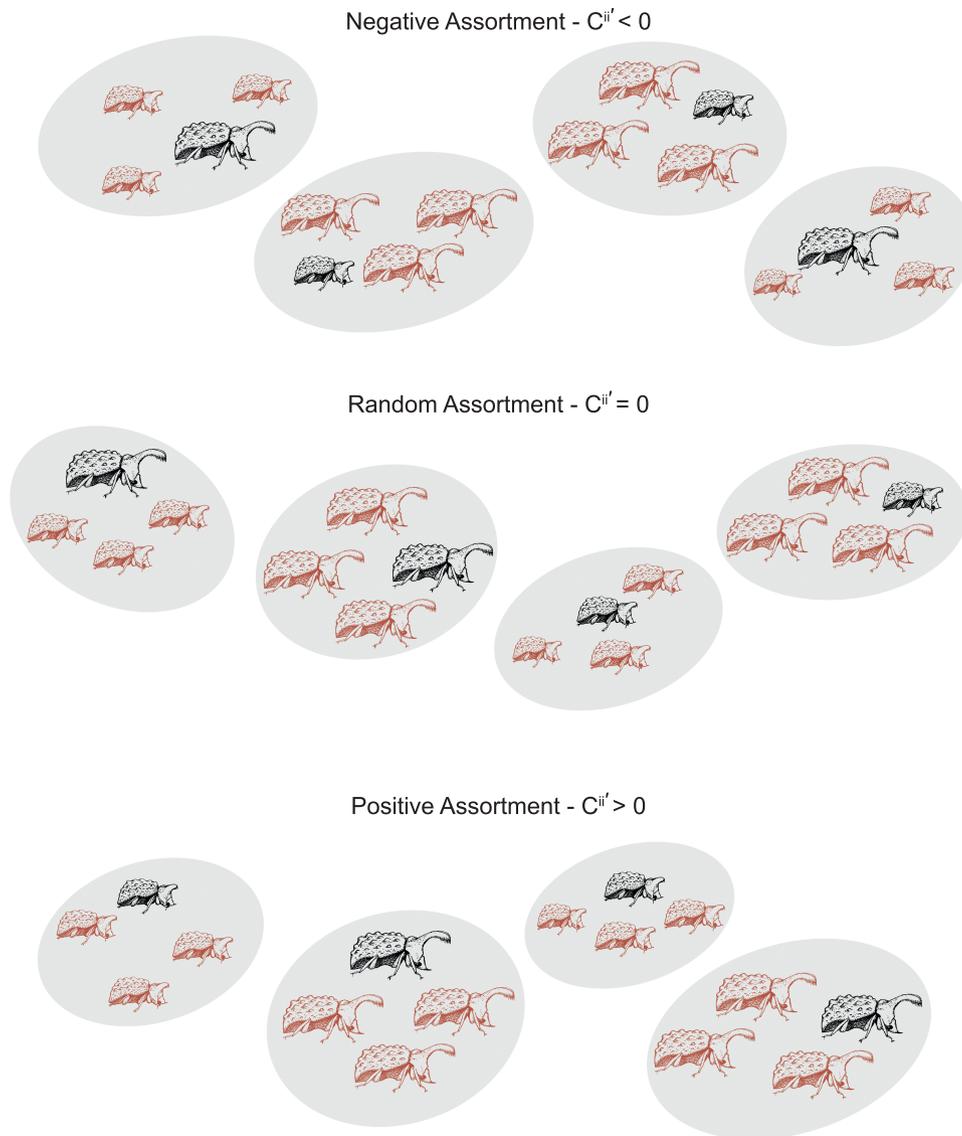


Figure 2. The interactant covariance $C^{ii'}$. The interactant covariance, or correlation, describes the phenotypic assortment between individuals and their social context. In this example, dark beetles are the focals, and lighter beetles represent all of the social partners with which they interact. The correlation shown is between the same trait (size) in the focal and the social context, $C^{ii'}$. At top, negative phenotypic association; in the middle, random assortment with respect to size; at bottom, positive phenotypic association.

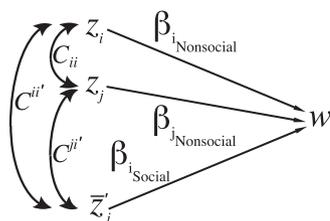


Figure 3. Multivariate path model of social selection. Individual fitness can be influenced by trait values of the focal, z_i and z_j through nonsocial selection gradients specific to each trait, β_N . Individual fitness can also be influenced by traits expressed in social partners, in this case noted as the average of all partners, \bar{z}_i , through social selection gradients, β_S . Phenotypic correlations between traits within the focal individual can cause correlated traits to experience indirect selection. Similarly phenotypic correlations between interacting pairs or groups of individuals, $C^{ii'}$ and $C^{ij'}$, can cause indirect effects of social selection.

be expected to have nonadditive effects on fitness, where the selection gradients depend on the combination of traits present in the focal and social partner (β_i), analogous to correlational selection (γ_{ij}) within individuals. These kinds of nonlinear selection gradients depend on the simultaneous values of traits in all interacting partners (or the “aggregate” character, $z\bar{z}$; Queller 1992b; Araya-Ajoy et al. 2020). These sorts of interactions, which are often frequency dependent, are often modeled in game theory treatments of behavior, such as when a Dove strategy would have different expected fitness interacting with another Dove than it would with a Hawk (McGlothlin et al., n.d.; Wolf et al. 1999; Westneat 2011; Araya-Ajoy et al. 2020). Though the selection and evolutionary response dynamics are somewhat different, the net effect of interaction selection gradients on phenotypic change is governed by an analogous form of the interaction covariance between a focal’s own phenotype and the simultaneous or aggregate values of the focal and its partners, $C^{i(ii')}$ (see equation 6 in Araya-Ajoy et al. 2020).

The path model decomposition of direct and indirect selection underscores one of the most critical points about phenotypic assortment and social selection. While the fitness effects of social selection are general and experienced by all conspecifics, the evolutionary consequences of social selection are specific to individual traits. The interactant covariance links selection gradients to specific traits that thereby experience indirect social selection. That means that even when social selection gradients are constant across time, space, or populations, the net effect of that selection on phenotypic evolution will vary depending on patterns of phenotypic assortment. Because each social selection gradient is multiplied by an interactant covariance term in both the total selection (equations 2 and 3) and response to selection equations (McGlothlin et al. 2010; Westneat 2011; Araya-Ajoy et al. 2020), phenotypic assortment can amplify, reverse, or erase the fitness effects that results from the phenotypic context. This range of effects of the interactant covariance has been observed in wild populations. Strong social selection sometimes results from interacting with larger bodied and more docile neighbors in eastern chipmunks (*Tamias striatus*), but no net effect on selection differentials emerges because of a lack of phenotypic assortment for these traits (Santostefano et al. 2019). Conversely, negative assortment with respect to body size in low-density populations leads to stronger net selection favoring larger body size in forked fungus beetles (*Bolitotherus cornutus*), in which large social partners generally reduce mating success of neighboring males (Formica et al. 2011a).

What Causes Interactant Covariances?

Ultimately, short-term evolutionary responses do not depend on what causes phenotypes in social partners to be correlated. As long as the statistical association between phenotypes of social partners exists, social selection will be transformed into indirect selection as outlined above. Moreover, the presence of a nonzero C^{ij} does not imply any particular underlying cause or active process. In fact, a wide range of direct and indirect factors including genetic, behavioral, and spatial phenomena can contribute to observed interactant covariances, and are interesting in their own right as some explicitly link social selection formulations to other classic problems in evolution and behavior ecology. These potential sources have been discussed at length elsewhere (Wolf et al. 1999; McGlothlin et al. 2010; Araya-Ajoy et al. 2020), so here we concentrate on the general patterns that lead to interactant covariance, and their unique impacts.

Active Assortment

Perhaps the most obvious way that phenotypes of partners can become correlated is through active trait-based behavioral associations. These might include choosing partners based on phenotypes, as takes place in mate or partner selection, or repelling or avoiding interacting with individuals with particular traits such as chasing away smaller neighbors, or avoiding larger competitors. The resulting C^{ij} might take any sign depending on the nature of the interaction and traits.

Often social assortment is based not on traits, but relatedness. Kin-based associations build phenotypic covariances because more closely related individuals tend to share common alleles across the genome, and therefore similar phenotypes (Queller 1992a, 1992b). This covariance of interactants is, of course, the basis of kin selection models and provides the connection between social selection models and the inclusive fitness/kin selection approach to understanding multilevel selection (Wolf et al. 1998, 1999; Cheverud 2003; McGlothlin et al. 2010). Kin-based associations always generate a positive C^{ij} between the same trait in social partners (although

other factors like behavioral plasticity or indirect genetic effects can overcome the positive covariance), so they invariably reinforce the direction of social selection on single traits. Again, this is why kin selection models favor altruistic or cooperative behavior within a generation—the benefit (i.e., positive social selection) is translated into positive indirect selection on the same trait through a $C^{ij} > 0$ (Queller 1985, 1992a, 1992b; Wolf et al. 1999; McGlothlin et al. 2010).

Kin-based assortment also has the effect of translating genetic architecture into congruous patterns of interactant covariance (see equation 12 in Wolf et al. 1999). Whatever additive genetic covariances that might exist among traits due to pleiotropy or linkage disequilibrium are faithfully converted into interactant covariances among the same traits when kin associate. The net effect is that kin-based assortment takes any patterns of indirect selection that occur at the individual level due to phenotypic integration and reinforces them through social selection gradients.

Active sources of interactant covariances are especially interesting because they represent possible mechanisms by which individuals can alter the impacts of social selection on phenotypic selection and their own fitness (Formica et al. 2004; Formica and Tuttle 2009; Saltz and Nuzhdin 2013; Saltz et al. 2016). This sort of social niche construction presents an opportunity for feedback between individual patterns of trait or kin-based interactions and population-level patterns of selection. Explorations of the importance of evolutionarily dynamic C^{ij} will be important steps forward toward understanding the links between selection and social behavior.

Passive Assortment

Interactant covariances can arise even when individuals do not actively determine their social partners. In these cases, passive or indirect effects of other patterns or processes can lead to nonrandom patterns of association. Because social selection is agnostic to the cause of C^{ij} , indirect sources of covariance have the same effects on evolutionary trajectories as active sources of covariance.

Subdivision or genetic structure within populations is likely to be one of the most important sources of C^{ij} (Wolf et al. 1999; Bijma et al. 2007; McGlothlin et al. 2010). Patterns of variable genetic relatedness in space mimic the effects of active kin-based association because local groups tend to share partners that are more closely related than they would be with individuals from the population at large (Queller 1992a, 1992b, 2011; Fisher et al. 2019). For example, a stand of plants with limited seed dispersal would be expected to have high local relatedness. As long as social interactions take place at a spatial scale that is congruous with the scale of subdivision, relatedness among partners should be higher than the population average and $C^{ij} > 0$.

Inbreeding increases average relatedness and the probability of shared genotypes, but its effect on patterns of phenotypic covariance of interactants is complex. Families or lineages that are inbred will have stronger interactant covariances than outbred ones if social interactions occur within families. However, population-wide inbreeding does not necessarily generate stronger C^{ij} because inbreeding increases relatedness equally among all pairs or groups of individuals (Wolf et al. 1999). As long as some patches or lineages are more inbred than others, and interactions are local or lineage specific, inbreeding can cause variation in similarity of partners and result in increased patterns of C^{ij} .

Trait-based habitat choice or environmental sorting leads to individuals with similar phenotypes inhabiting or using the same patches, so physical proximity is expected to generate positive interactant

covariances for the traits that are aligned with the original habitat choice (Wolf et al. 1999). If individuals choose a foraging habitat based on their morphology, or resting sites based on background matching to polymorphic color patterns, then they will generate phenotypic subdivision into groups of individuals with similar phenotypes ($C^{ii} > 0$). This kind of assortment is passive with respect to the phenotypes of the others in the same space, but rather a response to variation on another axis (e.g., matching background to their color pattern) based on individuals' own traits. Because we generally expect habitat choice to be adaptive, the traits that become correlated in this way are likely to enhance performance in the chosen habitat. One untested possibility is that the resulting competition among similar individuals could manifest as a negative social selection gradient, which would be reinforced by the positive C^{ii} .

Statistical artifacts of scale may also generate nonzero interactant covariances. The clearest example of this effect is the expectation that very small group sizes should generate negative interactant covariances for the same trait expressed by social partners (McDonald et al. 2017). Even when interactions among individuals are random and equal with respect to phenotype, negative interactant covariances can arise in small groups. This result obtains because deviations from the average must balance out among group members. In a very small group, a focal that is larger than the mean of the group must be interacting with individuals that are smaller than itself. This effect becomes negligible at large group sizes (McDonald et al. 2017). This bias has been used to argue that negative interactant covariances in small groups are not important to social selection because they do not require any deviation from null process to explain (McDonald et al. 2017). However, the existence of a negative C^{ii} reverses the direction of any social selection gradient resulting from the trait of interest, regardless of its cause. Small group size is thereby expected to reverse the sign of social selection on similar traits, in the absence of active processes (e.g., positive assortative mating in dyads) that ameliorate or outweigh the small group effect.

Phenotypic Modification

The third major source of phenotypic covariance among social partners is plasticity, or environmentally induced variation in trait expression. It is useful to divide the environment at the conspecific boundary. When the environmental influences are abiotic, or at least from other taxa, common environments cause individuals to express similar phenotypes. Social partners that share common environmental cues like temperature, or light, or the presence of predator odors, are likely to exhibit positive interactant covariances for traits that respond to those cues. Groups of offspring that experience common-family environments will have more similar phenotypes than offspring in a different environment, exacerbating the covariances that result from kin-based interactions. The magnitude of these kinds of common-family environments or maternal effects often decline with age (Wilson and Réale 2006), so we might expect the strength of interactant covariances within family groups to decline accordingly.

When the environmental effect stems from the phenotypes of conspecifics, more complex and recursive relationships between traits of social partners can emerge. This is the realm of interacting phenotypes and indirect genetic effects (i.e., ψ_{ij}) mentioned above. Any trait expressed by a neighbor that alters the expression of a trait, the same or different, in a focal individual, will generate phenotypic correlations among individuals. These correlations arise because variation in trait z'_j in a partner is causally related to variation in trait z_i in a focal. Despite the relationship to indirect genetic effect models, these interactions can be purely phenotypic and still alter the

interactant covariance. In other words, phenotypic variation does not have to be linked to additive genetic variation to influence the interactant covariance. Behavioral responses to other the actions of social partners, such as reciprocal cooperation or escalating territorial aggression, thereby result in phenotypic covariances between social partners. Increased growth rate in plants in response to the height of neighbors is another example that would lead to positive covariances between focals and social context. The sign of the resultant interactant covariance is not broadly predictable because it depends on the specific interactions among traits and individuals.

Measuring the Interactant Covariance

In the fundamental models that partition social selection, the important metric is the covariance between phenotypes of partners or interactants (Figure 2), which is equivalent to a correlation for variance-standardized traits (Wolf et al. 1999). This value can be simply estimated through variance component estimation or as a Pearson correlation. An alternative partitioning of selection gradients leads to a partial regression metric, which has been called an “assortment coefficient,” β_A , estimated as the slope of the regression of the social partner's phenotype on the phenotype of the focal (McDonald et al. 2017). If phenotypes are variance standardized, this assortment coefficient is equivalent to the correlation of interactants. The most important point in choosing a metric is that the scale must be consistent among selection gradients and association metrics, so that social selection and nonsocial selection sum to the accurate total.

The more subjective challenge is determining how to define “social partners” or “social group” and how to assess the social phenotype. The original models of social selection mostly assumed a single dyadic interaction with only one individual partner and one social-trait value for simplicity (Queller 1985, 1992a, 1992b; Moore et al. 1997; Wolf et al. 1999). This scenario clearly does not match biological reality in most systems, wherein multiple social interactions occur across lifetimes, may occur asymmetrically among individuals, and may have unequal impacts on fitness of focals. Ideally, the social phenotype represents the variation among focal individuals in the trait values they experience in the particular contexts that influence variation in fitness or a fitness component. For example, to understand intrasexual social selection on male mating success, it would be appropriate to consider all males with which a focal male might compete for mates. This goal might lead to at least a few different kinds of social contexts that could be considered—males that engage in direct interactions like fights or competition, males that share overlapping home ranges and thereby could be expected to interact, or all males that mate with a single female and experience postcopulatory competition within the reproductive tract of the female (e.g., Fisher et al. 2016).

The most common approach of quantifying social phenotype is to take an arithmetic mean of trait values across all of the identified social partners, \bar{z} . This mean can be weighted by the number of interactions with different individuals, if that resolution of information is available (Formica et al. 2021). More often, individuals are observed in a group of individuals that share space and time, and the average of that group is used as the social phenotype, without direct knowledge of how individuals may have interacted, such as with overlapping space use or simultaneous group membership (Formica et al. 2010; Fisher et al. 2017; Santostefano et al. 2019). An implicit assumption of this approach is that all conspecifics within the group or space have equivalent impacts on variance in

fitness. Social network structure offers the potential to include more complex information about the identity and relative importance of different partners (Farine 2014; Farine and Sheldon 2015). In this case, networks can reveal partner identity or weighting, but network assortment measures such as “assortativity” are not equivalent to the interactant covariance in evolutionary models, and should not be used to evaluate total selection differentials (McDonald et al. 2017).

Social selection analyses do not include the focal individual's trait value in the social phenotype estimate (an individual is not part of its own social group) and in this way differ slightly from contextual analyses that normally include all individuals in a group in contextual traits (Eldakar et al. 2010; Bouwhuis et al. 2015; Fisher et al. 2017) or treat the within-group trait as the deviation of the individual's trait from the group mean (Bijma and Wade 2008; Fisher and Pruitt 2019). This difference may seem minimal, especially for large groups, but only the social selection (or “neighbor”) approach allows the focal's phenotype to be uncoupled from the group, and thereby covary or not (Okasha 2004, 2013). Both contextual analysis and social selection are formulations of multilevel selection, in which individual fitness depends on properties of the group or social context it finds itself in, but social selection is unique in considering the importance of nonrandom associations in driving multilevel processes.

Empirical Studies of Variability of C^{ij}

Despite its importance in determining the shape of the multivariate adaptive landscape, there has been little investigation of the consistency or variability of the interactant covariance in natural systems. We know that phenotypic assortment occurs in many taxa, especially in the context of mate choice (Jiang et al. 2013). Recent exploration of animal social networks also has led to observations of assortativity based on phenotypic similarity, especially in fish and primates (Croft et al. 2005, 2009; Farine 2014; Carter et al. 2015; Zonana et al. 2019). But these studies tend to be largely phenomenological and meta-analyses suggest that the physical and temporal scale of observation can introduce variation in the strength of assortment at least among mating partners (Moura et al. 2021). Little other work is available to assess whether and how patterns of association among social partner phenotypes change across space and time, particularly in the context of the important evolutionary parameter C^{ij} . This problem is critical to understanding social selection because even if the fitness relationships that produce social selection stay constant, short-term changes in patterns of assortment could fundamentally alter the targets and modes of phenotypic selection.

To address some of these limitations, we assembled a range of data from wild and field-experimental studies of a beetle system with well understood modes of sexual and social selection. Forked fungus beetles (*Bolitotherus cornutus*) are long-lived insects that are obligately associated with polypore shelf fungus (*Gandoderma applanatum*, *G. tsugae*, and *Fomes fomentarius*) that grow on decaying logs and stumps throughout northeastern North America (Liles 1956; Pace 1967). Females lay eggs on fungus brackets, larvae live in and feed on fungus as they develop and then pupate, and adults aggregate on and around brackets for feeding and mating (Conner 1988, 1989; Formica et al. 2010, 2011a; Wood et al. 2014). Adults often live 2–3 years, and up to 5 (Wood et al. 2018). Male *B. cornutus* have thoracic horns that are used in same-sex aggressive competition over access to fungus brackets and potential mates (Mitchem et al. 2019). Subpopulations of *B. cornutus* are relatively viscous, with most adults remaining on the same log throughout

the active summer months, and often year-to-year (Whitlock 1992; Ludwig 2008; Wood et al. 2013, 2018). Social network analyses of adult interactions reveal high variability in the number of partners and connections among individuals, generating considerable variation in social context (Formica et al. 2010, 2011a, 2017, 2021).

We have studied a metapopulation of *B. cornutus* at Mountain Lake Biological Station in southwestern Virginia for over 10 years and here explore some of those data to investigate patterns of interactant covariance. In all cases, individual beetles were marked with unique tags and identified and scored directly by human observers. In most of the data that follow, both from the wild and seminatural field experiments, the location and behavior of every beetle was scored, as well as the identity of any social partner that was within 5 cm of a focal beetle. This proximity-based identification of social partners follows from the observation that individuals respond to conspecifics within that spatial range. We have used proximity partners in the past to construct social networks for forked fungus beetles (Formica et al. 2017, 2021). In one older data set from 2008, social partners were assigned based on shared space use because proximity partners were not directly identified in the original data collection (Formica et al. 2010, 2011b). We calculated social phenotypes as the average phenotype of all partners, weighted by the number of interactions with each partner. We focus here on the univariate interactant covariances, C^{ij} , that occur between the same morphological traits (overall size or horn length) of males in focals and partners.

Male horn length and body size are highly variable and tightly correlated within individuals (Formica et al. 2011a, 2021). Previous studies of aggressive interactions and mating success in our study population and others, from both wild and staged captive scenarios, indicate that larger, longer horned males tend to win fights, gain more access to mates, and successfully copulate more often (Conner 1988, 1989; Formica et al. 2011a, 2021; Mitchem et al. 2019). The fitness advantages to large males, $\beta_N > 0$, are chiefly obtained in low-density subpopulations and typically disappear when the density of males exceeds one per bracket (Conner 1989; Formica et al. 2011a). Given this competitive social environment, it is not surprising that social selection that depends on the overall size of social partners has been detected (Formica et al. 2011a, unpublished data). Males with social neighborhoods that include large beetles have reduced mating success, observable as a negative social selection gradient, $\beta_S > 0$, on partner body size or horn length. This general trend of positive nonsocial and negative social selection on size or horn length has been detected in multiple subpopulations and years (Formica et al. 2021, unpublished data).

So how does this social selection gradient affect the total phenotypic selection on male body size or horn length in forked fungus beetles? The answer depends, of course, on the pattern of phenotypic assortment.

Field observations provide a picture of the variability in the interactant covariance in unmanipulated natural subpopulations. These subpopulations represent a wide range of different environmental and social variables including the number and density of resident beetles, the amount of fungal resources, the species and distribution of host fungus, and a myriad of other physical properties (Formica et al. 2021). Estimates of interactant covariances that emerge from these field data represent the full range of variation we might expect in freely associating individual forked fungus beetles.

We estimated C^{ij} for 6 subpopulations that were sampled 3 times a day for at least 60 days in 2 successive years (2016 and 2017). The subpopulations ranged in size from 34 to 331 individuals (males and females), but not all individuals were observed to

have social partners, so estimates are based on a total of 146 males in 2016 and 126 males in 2017. Pooling across all focal males in the metapopulation, Pearson correlation coefficients reveal no observable phenotypic association based on horn length ($C^{ii'}_{2016} = 0.04$, $P = 0.54$; $C^{ii'}_{2017} = -0.05$, $P = 0.51$). However, some subpopulations showed strong patterns of association, and these ranged from strongly negative ($C^{ii'} = -0.49$) to strongly positive ($C^{ii'} = 0.43$). This variability in how males associated based on horn length could be explained by local social or environmental influences, or could reflect a simple lack of consistency in assortment. We therefore asked whether subpopulations (i.e., logs) were consistent in their pattern of phenotypic assortment across years. Subpopulation differences were remarkably consistent ($r = 0.58$; Figure 4). Only one of the 6 subpopulations changed sign of $C^{ii'}$, and the most strongly negative and positive associating subpopulations remained so. We found this consistency surprising, because different focal males were present across years, and a variety of demographic variables including population size changed in that time.

One factor that has been shown to be important in the strength of sexual and social selection in forked fungus beetles is male density (Conner 1989; Formica et al. 2011a). Presumably, higher density leads to more fighting among males that in turn reduces the relative advantage to more aggressive and competitive males. In a study that used overlapping space use (not proximity partners as above) to explicitly examine social selection on a multivariate size score (the first principal component including elytra length, horn size, and pronotum width), the size of social partners was found to reduce focal fitness across the pooled metapopulation ($\beta_s = -0.36$; Formica et al. 2011a). A weak but significant negative interactant covariance was also detected at the pooled metapopulation level ($C^{ii'} = -0.16$). These patterns were more exaggerated in low-density subpopulations (<1 male/bracket), and effectively absent in high-density ones ($r = 0.95$; Figure 5). The pooled $C^{ii'}$ for the 3 low-density populations was -0.53 , and essentially zero for the high-density populations (Formica et al. 2011a). The effect of this strong negative interactant covariance coupled with strong negative social selection on body size is a net increase in the total strength of phenotypic selection on body size of almost 50% in low-density subpopulations. It has been suggested that small social group size explains the negative interactant

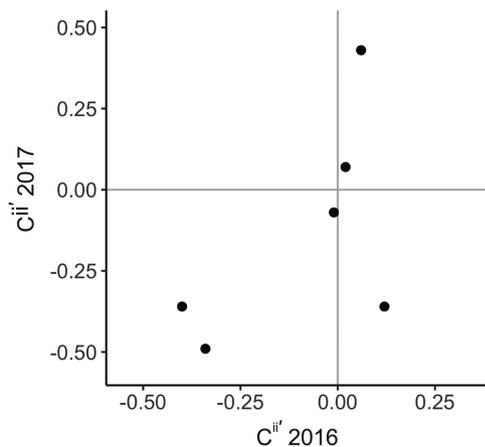


Figure 4. Long-term consistency in $C^{ii'}$ of male thoracic horn size. Six natural subpopulations were sampled in subsequent years (2016 and 2017). Male patterns of assortment based on thoracic horn length varied from strongly negative to strongly positive, but subpopulations retained their general patterns of assortment year to year ($r = 0.58$).

covariance in this example (McDonald et al. 2017). Regardless of the source of the negative interactant covariance, it contributes to the total indirect social selection on body size in the same way.

Although the data from wild subpopulations give a sense of the variability in phenotypic assortment under natural conditions, too many factors vary across these groups to determine what causes differences in the interactant covariance. To gain some insight into these causal factors, we take advantage of some manipulative experiments conducted under seminatural conditions. We constructed large walk-in screen enclosures (“beetleeries”) set in the forest and stocked them with farmed fungus arrayed in a grid that represented an artificial log. We grew fungus in the laboratory from a single genotype of *G. tsugae* that produced uniform size and age brackets on bags of sawdust. We then deployed these brackets in the beetleeries, allowing us to manipulate resources as well as social properties of each experimental population in a replicated fashion. Each experimental population of beetles was constructed with equal sex ratio and a phenotypic distribution of elytra length that mimicked the mean and variance of the natural distribution. Social partners and social phenotype data were collected in the same way as data from the natural populations.

Because resource distribution is expected to mediate movement and therefore social connectivity of individuals within a population or social network, we conducted a manipulation that varied only the spatial distribution of fungus brackets. Brackets were arrayed in either a clumped or even distribution, holding constant the total resource and demographic properties (Costello et al., unpublished data). Twelve experimental populations were set up at intermediate density (1 male/bracket) with 18 males and 18 females. Every group of beetles experienced both treatments for 3 weeks in a random order. We pooled populations within each treatment to ask if there were overall effects of resource on patterns of phenotypic assortment (Figure 6). When beetles were exposed to clumped resources, they did not assort with respect to horn length ($C^{ii'} = -0.11$, $P = 0.11$). When the same groups of beetles experienced distributed resources, they increased their home range sizes, which in turn caused beetles to interact less often and with fewer partners (Costello et al.,

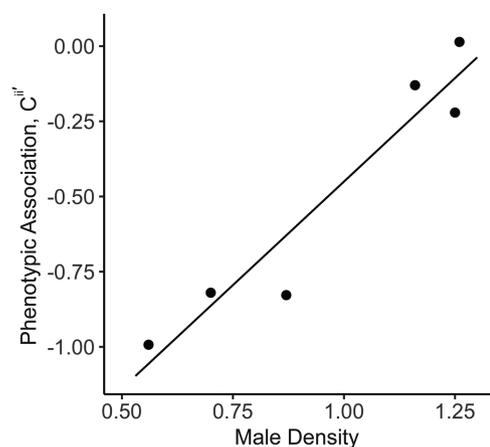


Figure 5. Density effects on $C^{ii'}$ of body size of male forked fungus beetles. Subpopulations exhibited variable patterns of assortment with social partners based on a multivariate size index (principal component 1 of morphological measures) that correlated with local density ($r = 0.95$). In low-density subpopulations with fewer than 1 male per fungus bracket, males overlapped home ranges with opposite sized males. In higher density populations, no pattern of phenotypic assortment was detected (data from Formica et al. 2011a).

unpublished data). In these conditions, they exhibited a moderately negative and significant interactant covariance ($C^{ii} = -0.20$, $P = 0.007$). These results indicate that patterns of phenotypic assortment are sensitive to features of the physical environment, and can change on fairly short time scales.

In a second experiment, we manipulated the social personalities of the individual beetles that comprised each group (Cook et al. unpublished data). Using the same clumped resource distribution as above, 10 beeteries were stocked with slightly lower density populations than the previous experiment (15 males and 15 females, 0.83 males/bracket) and observed 3 times a day for 8 days (Figure 7). In this initial, randomly distributed group of personalities, males exhibited a moderate negative interactant covariance ($C^{ii} = -0.21$, $P = 0.05$), in contrast to the random distribution previously observed at higher density under the same resource distribution. After the first round, beetles were collected, isolated, and reassigned based on the number of social interactions they exhibited in the first round. Two social treatments were generated—5 replicates of highly social beetles (that experienced an average of 10 interactions during the first 8 days) and 5 replicates of less social beetles (that experienced an

average of 4 interactions during the first 8 days). The groups of less social beetles had fewer interactions and were less connected than the groups of more social beetles. The populations of less social beetles did not assort based on horn size ($C^{ii} = -0.15$, $P = 0.42$), whereas the more social beetles reversed the sign of association and assorted strongly positively ($C^{ii} = 0.41$, $P = 0.0015$). This rapid change in the interactant covariance indicates that the individual personalities in a group can dramatically shift the patterns of assortment and thereby the total strength of phenotypic selection in short order.

This rather haphazard collection of estimates of interactant covariances points to several trends with consequences for patterns of phenotypic selection. First, C^{ii} varies enormously in sign and magnitude at a local scale, at least in highly structured metapopulations like those of forked fungus beetles. Differences in the interactant covariance among subpopulations mean that even consistent fitness effects like the cost of interacting with large horned social partners will have different effects on the evolution of horn length. These differences at the local level could in turn generate the potential for multilevel social selection not through difference in phenotype–fitness relationships, but in the sign of interaction covariances. The net force of selection that affects the morphology of an individual beetle depends on the subpopulation that it finds itself in.

Patterns of assortment among social partners appear to be highly and quickly plastic in response to environmental and social changes, changing on the scale of days when major changes occur (or are imposed experimentally). Generally speaking, situations with more interactions among individuals (higher density, more social personalities, more clumped resources) all seemed to have less negative C^{ii} , which in turn contributes to stronger net selection for increased horn or body size at the population level. We suspect that this trend emerges because high levels of interaction mean that individuals experience more partners and therefore a more random sample of possible phenotypes. In the forked fungus beetle system, high density and high sociality may limit the ability to choose (or avoid) particular partners that allow negative interactant covariances to arise. On the other hand, the highly social groups engineered in the experiment above, which exhibited the highest numbers of social interactions, actually assorted positively with respect to horn length suggesting a different behavioral dynamic is at play.

This lability of assortment is somewhat hard to consolidate with the observation that subpopulation-level differences are broadly consistent from one year to the next. We know that turnover in individual membership takes place during this time frame, and that individuals express consistent social tendencies even when group membership changes (Cook et al., unpublished data), leading us to expect limited consistency in patterns of association. Local abiotic and biotic conditions clearly drive some of the variance in the interactant covariance and the observed patterns suggest they may lead to long-term stability at the level of logs. How temporal changes in association will translate into multigenerational change is unclear. If the changes track predictable trajectories of resource decline or distribution, or the demographic of populations, then changing C^{ii} might represent a novel dimension of eco-evo dynamics driven not by phenotype–fitness relationships, but by patterns of association.

The long-term evolutionary consequences of local and temporal variation in phenotypic association depend on the strength and scale of subdivision in the metapopulation. At one extreme, local differences would be washed out if the individuals mix and mate randomly at the metapopulation level each generation. At the other, limited migration among demes sets up opportunity for adaptation to local social environments. The picture of subdivision in forked

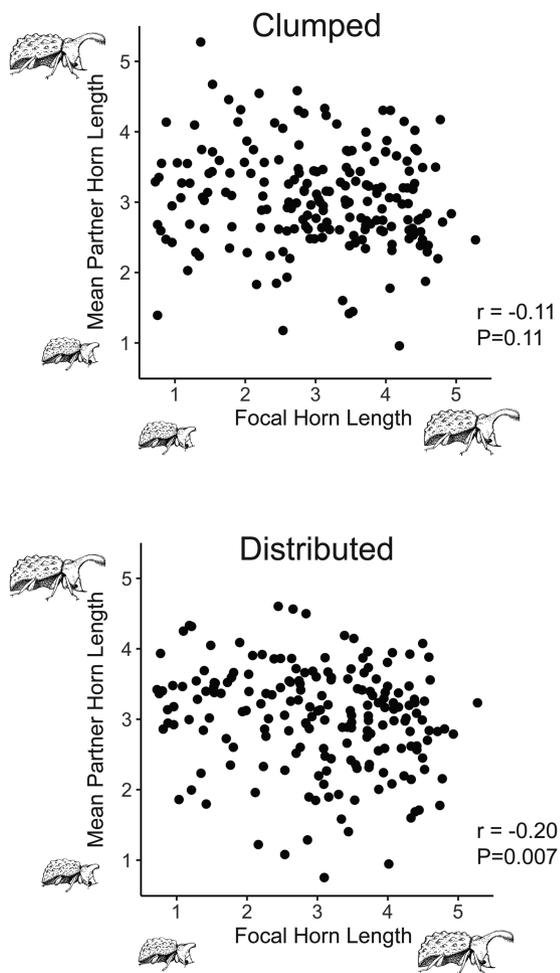


Figure 6. Effect of resource distribution on C^{ii} of male horn length. In experimental populations of randomly assigned groups of 36 beetles with equal sex ratio, males showed no significant patterns of size based assortment when fungus resources were clumped (top). When resources were evenly distributed in space (bottom), the same groups of beetles showed moderate negative assortment based on horn size.

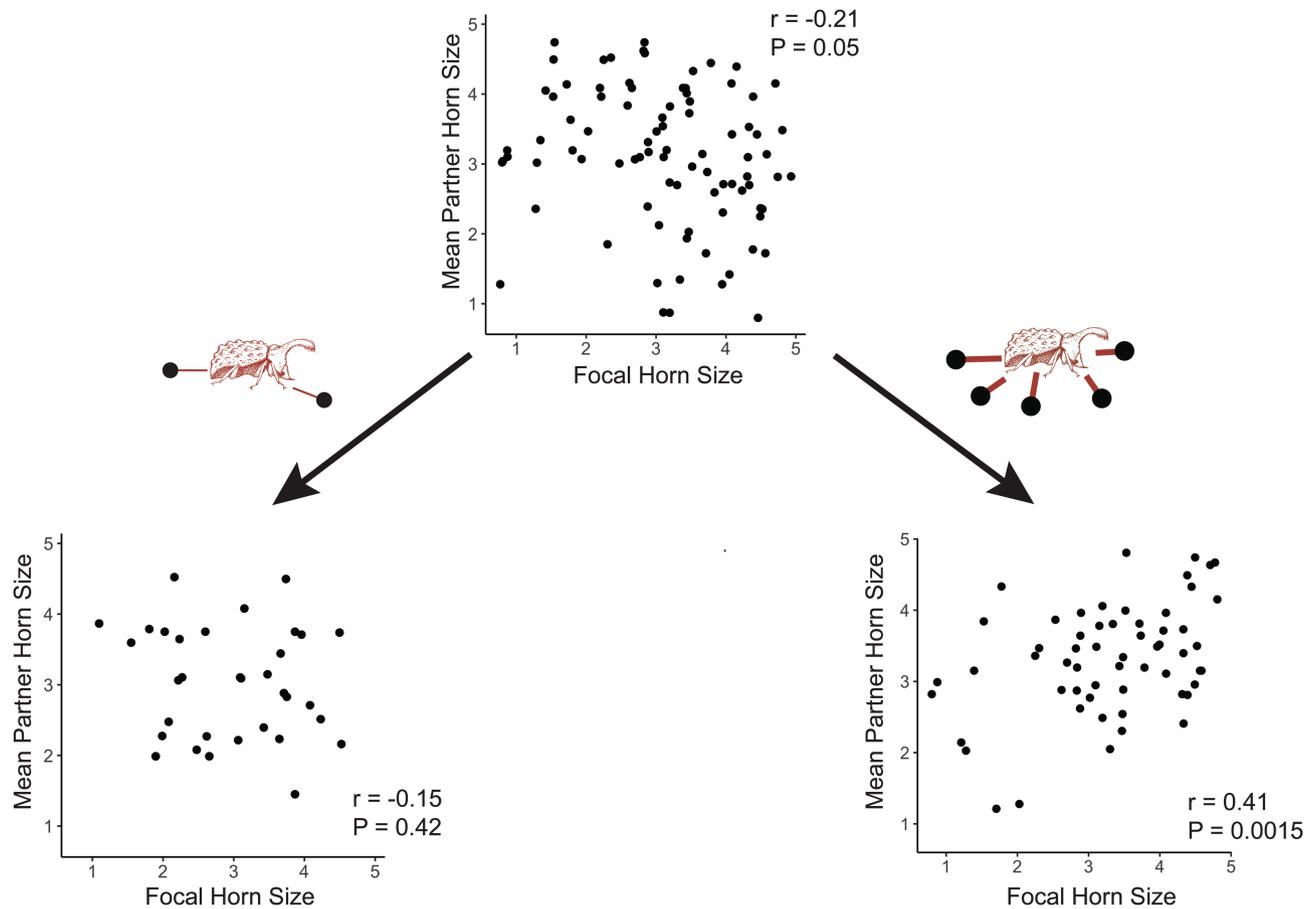


Figure 7. Effects of social manipulations on C^{ij} . In experimental populations of randomly assigned groups of 30 beetles with equal sex ratio, males showed moderate negative assortment on the basis of horn size (center top). When less social (left) and more social (right) beetles from this first round were grouped together, the more social beetles reversed the sign of their associations, grouping with similarly sized males (right).

fungus beetles metapopulations is not clear. Even with the Mountain Lake metapopulation, some studies indicate relatively strong F_{ST} (Whitlock 1992) and limited individual movement (Ludwig 2008) among logs (subpopulations), while others show no genetic subdivision (Wood et al. 2013) and higher levels of individual movement (Wood et al. 2018). Discerning the true evolutionary consequence of local variation in phenotypic assortment likely requires a more quantitative consideration of temporal scales of change, relative subpopulation densities, as well as overall genetic subdivision.

Conclusions

Phenotypic assortment among social partners plays a major and underappreciated role in determining the multivariate landscape of selection. Many of the most important questions about C^{ij} are empirical and require estimates from a variety of systems and contexts. We presented a small survey of estimates that indicate variability in patterns, but all from a single species of insect in one metapopulation. If C^{ij} is consistently expressed across time and space, C^{ij} could be a primary determinant of how the fitness effects of social interactions determine phenotypic evolution. On the other hand, if the critical patterns of assortment are highly labile and unpredictable, they will essentially erase the long-term consequences of social selection. To assess this general impact, we need repeated estimates of C^{ij} across populations and across time within populations from as many natural systems as possible. Understanding the relative importance of

extrinsic and intrinsic contexts in creating variation in phenotypic assortment will go a long way toward determining the evolutionary role of the multivariate C^I matrix.

A critical step in understanding phenotypic assortment is determining the appropriate physical and temporal scales of assortment. Defining an individual's social context is deceptively complex. Do arithmetic means of all social partners accurately represent the relative importance of those phenotypes in determining variance in fitness and the targets of indirect selection? Or should estimates be weighted by frequency or quality of interactions or network connections? Even deciding on which individuals should count as partners is difficult and depends on the biology of each system. For some species, physical interactions might be appropriate, in others proximity or shared space use, or even overlapping home ranges, might be more representative if indirect cues like territory markings convey social information and fitness consequences. Whatever the social definition of a partner or context, we then have to determine the time scale over which interactions are important, be it lifetime, a single breeding season, or some shorter definable unit.

Finally, whether and when C^{ij} evolves has important implications for phenotypic evolution in social contexts. Any good adaptationist expects selection to favor individuals that behave, move, and distribute themselves in ways that ameliorate the negative effects and reinforce the positive effects of social interactions. Indeed, this general sort of assortment is the basis of much of behavioral ecology, from the ideal free distribution to evolutionary games. If patterns of

phenotypic assortment can evolve, through any of the causal pathways mentioned earlier, then C^{ij} may become an adaptive strategy that mediates social selection (e.g. Araya-Ajoy et al. 2020). Because it connects general social selection gradients to specific axes of the phenotype, evolving aspects of C^{ij} might thereby generate predictable feedbacks between social selection and the multivariate phenotypic selection landscape.

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Data Availability

All original data are available on Dryad <https://doi.org/10.5061/dryad.sqv9s4n54>.

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