



Invited Review

Indirect genetic effects in behavioral ecology: does behavior play a special role in evolution?

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Received 1 June 2017; revised 17 August 2017; editorial decision 25 August 2017; accepted 21 September 2017.

Behavior is rapidly flexible and highly context-dependent, which poses obvious challenges to researchers attempting to dissect its causes. However, over a century of unresolved debate has also focused on whether the very flexibility and context-dependence of behavior lends it a unique role in the evolutionary origins and patterns of diversity in the Animal Kingdom. Here, we propose that both challenges can benefit from studying how indirect genetic effects (IGEs: the effects of genes expressed in one individual on traits in another individual) shape behavioral phenotypes. We provide a sketch of the theoretical framework that grounds IGEs in behavioral ecology research and focus on recent advances made from studies of IGEs in areas of behavioral ecology such as sexual selection, sexual conflict, social dominance, and parent–offspring interactions. There is mounting evidence that IGEs have important influences on behavioral phenotypes associated with these processes, such as sexual signals and preferences and behaviors which function to manipulate interacting partners. IGEs can also influence both responses to selection and selection itself, and considering IGEs refines evolutionary predictions and provides new perspectives on the origins of seemingly perplexing behavioral traits. A key unresolved question, but one that has dominated the behavioral sciences for over a century, is whether behavior is more likely than other types of traits to contribute to evolutionary change and diversification. We advocate taking advantage of an IGE approach to outline falsifiable hypotheses and a general methodology to rigorously test this frequently proposed, yet still contentious, special role of behavior in evolution.

Key words: behavioral plasticity, interacting phenotype, interaction coefficient ψ , sexual conflict, sexual selection, social behavior.

“Thus, behavior being especially plastic, behavior must often take the lead in evolution.” Mary Jane West-Eberhard (2003), p. 180

INTRODUCTION

Is behavior special?

Those who study animal behavior are often motivated by the observation that behaviors can appear to be counterintuitive, making it necessary to dissect and reveal their costs and benefits, plus the trade-offs inherent in long-lived organisms. This has often been approached using an optimality framework, which defines evolutionarily stable outcomes under such conditions (Parker and Maynard Smith 1990). Classic examples of counter-intuitive behaviors that have been studied using optimality include sexual cannibalism, conspicuous sexual signaling, altruism, and aggression. However, this framework has a potential limitation. Optimality treats such behaviors as an emergent property of many

underlying, potentially unknown or even unknowable, mechanistic influences on different constituent traits—an approach that Grafen (1984) described as a phenotypic gambit, where the necessary mechanisms including genetics are assumed to allow unconstrained evolution to an optimum. Ignored causal influences range from molecular signaling pathways, to morphological structures, to nervous connections, to environmental context. Thus, the phenotypic gambit has significant limitations (Moore and Boake 1994; Golmulkiewicz 1998; Hadfield et al. 2007; Rubin 2016), not the least of which is ignoring evolutionary dynamics on the way to an equilibrium (regardless of whether it is reached). It is perhaps ironic that behavior appears to be one of the least suited types of traits to study using this framework (Roff 1996; Fawcett et al. 2013). This may be due in part to the high degree of reversibility and context-dependence of many behaviors, particularly those expressed in the context of social interactions.

It may be that the simultaneous integration of many different causal factors is what makes behavior such a challenging phenotype to study mechanistically: behavior can be highly reversible, variable, inconsistent, contextual, and ephemeral. Yet, the complexity of inputs to behavior may also contribute to its alleged special nature. For well

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over a century, its flexibility and environmental sensitivity have been invoked to support a special role in evolution, for example by biasing the direction of evolutionary responses (Baldwin 1902), exposing new variation to the action of selection (Wcislo 1989), acting as a pacemaker that regulates the rate of diversification (Mayr 1963), disproportionately leading genetic evolution (West-Eberhard 2003; Zuk et al. 2014; Robinson and Barron 2017) or inhibiting evolution (Huey et al. 2003; Price et al. 2003). Unusual roles for plasticity and behavior have also been invoked to argue for reformulating the fundamental structure of evolutionary theory as we know it, an assertion that has provoked scepticism and contentious debate (Laland et al. 2014). Arguments for behavior's special role in evolution often invoke mechanisms such as genetic assimilation, accommodation, or shifting plasticity thresholds to link nongenetic behavioral variation to longer-term genetic evolution. Such processes have theoretical backing (e.g., Lande 2009; Chevin and Lande 2015), and some empirical support (e.g., Waddington 1953; Badyaev 2009; Sikkink et al. 2014). Verbal arguments have suggested that the link between behavior and evolution is expected to be strongest in circumstances where behavior is sensitive to variation in the social environment (e.g., Bateson 2004), and social effects have been proposed to play a correspondingly greater role in behavioral evolution in species with highly complex social interactions, such as the eusocial Hymenoptera (Linksvayer 2015).

In this article, we describe how behavioral ecologists are increasingly adopting a research approach that considers genes expressed in social partners—indirect genetic effects, or IGEs—to be a part of the environmental context that shapes animal behavior. We explore how IGE frameworks provide behavioral ecologists with tools to improve optimality predictions and obtain more focused solutions to research challenges, for example by better understanding the causes of behavioral variation within and between species. We suggest that empirically examining the role of IGEs in shaping behavior will provide important insights for the field of behavioral ecology. Beyond this, however, we suggest a methodological approach using IGEs to rigorously test whether behavior does, or does not, play a unique role in evolution.

BEHAVIOR AND IGEs

The reversibility, context-dependence, and sensitivity of behavior

Competing definitions of behavior abound, but one commonly accepted defining characteristic is that behavior entails a response to environmental stimulus (Levitis et al. 2009). Thus, flexibility or plasticity is an inherent property. This flexibility has led to the well-known debate over nature and nurture, where simple causes (genes) are rightly viewed as insufficient explanations for the expression of a behavioral phenotype. Of course, this reflects a false dichotomy (both nature and nurture must contribute for any trait to exist) but it also reflects a sense that there is inherent complexity in behavior that may not exist in other phenotypes. Incorporating IGEs allows nature to be nurture as well, resolving some of these concerns (Moore et al. 1997; McGlothlin et al. 2010). Social interactions induce IGEs, which partly explains why the flexible properties of behavior make it prone to unexpected evolutionary dynamics or phenotypic equilibria that can appear nonadaptive. The apparent susceptibility of behavioral phenotypes to social influences could make them especially prone to IGEs, providing a testable, though presently hypothetical, evolutionary genetic explanation for their proposed role in evolution.

What are, and are not, IGEs?

A framework for studying behavior was specifically developed to incorporate genetics and further refine the evolutionary understanding of traits identified as fundamental in behavioral ecology—the Interacting Phenotype approach (Moore et al. 1997, 1998). This approach incorporates IGEs, and it recognizes that many of the attributes that make understanding behavioral evolution difficult arise from behavior expressed in social interactions. This characteristic is part of what generalizes and extends IGE models from maternal effects, which are a specific case of IGEs (Wolf et al. 1998; McAdam et al. 2014).

IGEs result in altered evolutionary trajectories (Moore et al. 1997; McGlothlin et al. 2010). Examples where social environments and IGEs are predicted to affect trait expression and evolution involve interacting phenotypes such as communication, signaling, aggression, dominance, learning, sexual conflict, and sexual selection (Moore et al. 1998; Bleakley et al. 2010; Wolf and Moore 2010). But despite the intended connection to behavioral ecology, research on IGEs has until recently been concentrated in the fields of quantitative and behavioral genetics. From such studies, we know that variation in the social environment animals experience can generate evolutionary feedbacks mediated by IGEs if the social environment consists of genetically varying individuals; such feedbacks arise because the environment itself can evolve (Moore et al. 1997; Bailey 2012). The strength and direction of IGEs can also evolve over time and across populations (Chenoweth et al. 2010; Bailey and Zuk 2012; Kazancıoğlu et al. 2012; Ednbrow et al. 2017), and associated social selection is predicted to vary accordingly (McGlothlin et al. 2010). In recent years, IGEs have been incorporated into animal and plant breeding studies to more accurately predict evolutionary responses in agriculturally valuable traits, such as growth rate, thermal tolerance, and infection risk (Camerlink et al. 2013, 2014, 2015; Costa e Silva et al. 2013; Anche et al. 2014; Muñoz et al. 2014; Alemu et al. 2016; Baud et al. 2017). A substantial literature explores the mathematical approaches used to study IGEs. For general overviews see Bleakley et al. (2010), Wolf and Moore (2010), and McAdam et al. (2014); for a treatment of quantitative modeling and parameter estimation issues, see Bijma (2010, 2014).

IGEs do not require a conceptually new entity. These are additive genetic effects in individuals that contribute to a social environment that affects the trait of another (focal) individual, and which can itself evolve. As noted by West-Eberhard (1979 p. 228) when discussing social evolution and extravagant characters, "... a change improving competitive ability is always favored... Each successive improvement sets a new standard which the next can profitably surpass. This is due to the fact that conspecific rivals are an environmental contingency that can itself evolve. In that respect social evolution is comparable to the coevolution of predator-prey, parasite-host interactions..." Thus, evolutionary biologists have long recognized social environments as providing novel evolutionary dynamics. Because of IGEs, contributions to social traits can covary genetically, even when the genes act in different individuals. It is this covariance that results in unusual evolutionary dynamics. When an individual expresses a behavior, that phenotype reflects the inherent properties of the individual (e.g., physiological state, genes, experiences, and learning) as well as external abiotic and biotic influences. However, when the environment is social, then genetic differences among these interacting individuals contribute to differences in the social environment, creating a heritable

environmental effect. In other words, genes and the environment are confounded. Heritable social effects create nonlinear evolutionary dynamics when incorporated into evolutionary models (Moore et al. 1997; McGlothlin et al. 2010). When specific phenotypes are being studied, the interaction coefficient, ψ (Ψ), describes the importance of the interaction for the phenotype that is expressed. For traits unaffected by social interactions, $\psi = 0$. In traits where the social interaction reduces trait expression, $\psi < 0$, but where traits are increased in expression because of the social interaction, $\psi > 0$. Box 1 illustrates the concept and highlights recent studies that have estimated ψ or its multivariate counterpart, Ψ .

BOX 1. THE INTERACTION COEFFICIENT, Ψ : A STANDARDIZED ESTIMATOR OF IGES WHEN TRAITS ARE KNOWN A PRIORI

Trait-based approaches for estimating IGes focus on how previously identified traits interact, and therefore require more emphasis on a priori hypotheses. Focal and interacting behaviors are frequently known in advance in behavioral ecology studies, which may account for the increasing popularity of estimating ψ . Other resources provide detailed mathematical treatment of ψ and guidance on how to estimate it (e.g., Bleakley et al. 2010; Schneider et al. 2017), so we confine our remarks to a brief conceptual overview highlighting the importance of the parameter (and its multivariate counterpart, Ψ) plus several recent studies that have estimated it.

A significant advantage of estimating ψ , as opposed to utilising the variance-partitioning approach of quantifying IGes outlined in Box 2, is that it does not necessarily require detailed genetic information. The parameter was originally derived as an analogue of the maternal effect coefficient, m , and can be estimated by regressing standardized phenotypic values of focal genotypes on the trait values of their interacting partners (Moore et al. 1997). If trait values are mean centered with unit variance prior to entry into such a model, then ψ_j is the partial regression coefficient describing how trait i in focal individuals covaries with trait j in interacting partners. The resulting estimates of ψ range from $(-1,1)$ and indicate both the magnitude and direction of IGes. Reciprocal trait interactions occur when the same trait is examined in both individuals, and the matrix Ψ reflects all pairwise and reciprocal trait interactions when more than one trait is measured. Thus, IGes can be quantified conveniently in studies where it is possible to manipulate genotypes using different strains or inbred lines. Even when strains or lines are not readily available, as often occurs in behavioral ecology studies, other means for partitioning genetic variation in interacting partners can be used, for example by taking advantage of naturally-occurring alternative phenotypes with a genetic basis (e.g., Bailey and Zuk 2012). An equation adapted from 2 recent studies (Marie-Orleach 2017; Signor et al. 2017), derived originally from Moore et al. (1997), is illustrative:

$$z_i = \alpha_i + \gamma_i l + \sum_{j=1}^n \psi_{ij} z'_j + \sum_{j=1}^n \gamma_{ij} (l \times z'_j) + \epsilon_i \quad \text{Eqn. 1.1}$$

This model describes how the expression of a trait in a focal individual, z_i , is affected by IGes caused by interaction with

BOX 1. Continued

social partners, z'_j . For every trait j in the interacting partner, the magnitude and direction of IGes on trait i in the focal individual can be estimated by ψ_{ij} . Studies of behavior can often take advantage of distinct genetic strains or inbred lines, and one way to measure line-specific values of ψ is to run separate models for each line (e.g., Signor et al. 2017). In the example above, however, estimates of ψ_{ij} are modeled simultaneously for different focal lines by examining the interaction between a main effect of focal line, l , and z'_j for each interacting trait. Errors and intercepts are given by ϵ_i and α_i , respectively. More complex models can be built upon this framework, for example multivariate formulations in which relationships between multiple focal and interacting traits $z_{i..m}$ and $z'_{j..m}$ can be captured by an $m \times m$ matrix (a square matrix when the same suite of traits is measured in both focal and interacting individuals; the diagonal entries representing reciprocal trait interactions):

$$\Psi = \begin{bmatrix} \psi_{1,1} & \cdots & \psi_{1,m} \\ \vdots & \ddots & \vdots \\ \psi_{m,1} & \cdots & \psi_{m,m} \end{bmatrix} \quad \text{Eqn. 1.2}$$

Critically, ψ (and in the multivariate case, Ψ) are key determining factors of the unique dynamics caused by IGes. For example, the interaction coefficient plays a critical role in determining the consequences of IGes in models of sexual conflict (Moore and Pizzari 2005), Fisherian sexual selection (Bailey and Moore 2012), and the evolution of IGes themselves (Kazancioğlu et al. 2012).

Genetically distinct strains of study animals have been used in a variety of systems to estimate ψ . Such studies vary in the level at which genetic differences between interacting partners are manipulated. At one extreme, population-level differences in ψ for a component of female mate choice in the field cricket *Teleogryllus oceanicus* rests on the assumption of population genetic structure, and therefore provides inference about differences in IGes at the population level (Bailey and Zuk 2012). In contrast, several studies provide strain-specific estimates of ψ , for example for predator avoidance behaviors in the guppy *Poecilia reticulata* (Bleakley et al. 2009), sexually antagonistic mating behaviors in the hermaphroditic flatworm *Macrostomum lignano* (Marie-Orleach et al. 2017), and locomotion in the fruit fly *Drosophila melanogaster* (Signor et al. 2017). The latter 3 studies used a small number of inbred lines and report that ψ not only varies for different behavioral traits, but also that different lines show different values of ψ . Earlier work also used experimental evolution in lines of *D. serrata* to demonstrate evolution of ψ for sexually-selected cuticular hydrocarbon profiles (Chenoweth et al. 2010). In *D. melanogaster*, a multiple regression approach was used with 50 interacting, inbred lines from the *Drosophila* Genetic Resource Panel to identify candidate interacting traits affecting focal male tapping behavior, which was demonstrated to be affected by IGes but required interrogation to identify traits involved with the IGE (Bailey and Hoskins 2014). While there is clearly heterogeneity in the approach for manipulating the genotype of interacting individuals in such studies, the use of a common, standardized estimator allows comparison of the relative importance of IGes across different species, traits and contexts.

The importance of timing and sequence in social interactions

The timescale over which individual phenotypes change because of IGEs influences the outcome of evolutionary dynamics, depending on the number and frequency of social interactions (McGlothlin et al. 2010; Saltz 2013; Schneider et al. 2017; Anderson et al. 2017; Edenbrow et al. 2017). In addition, the phenotypic equilibrium for a trait affected by IGEs is determined partly by the whether the IGE is reciprocal or not (i.e., the same trait influences its own expression in focal and partner individuals, as in aggressive escalations, versus a focal trait that is affected by a different trait in an interacting partner, as in maternal care). When IGEs are particularly strong and reciprocal, theoretical arguments have predicted that the trait equilibria of phenotypes involved become unstable, possibly leading to increasingly extreme phenotypic fluctuations, oscillations, or even the disintegration of social groups (Trubenová et al. 2015).

The influence of timing of social interactions has been considered most extensively in the context of agonistic encounters and animal contests. For example, aggressive conflicts between groups of green woodhoopoes (*Phoeniculus purpureus*) that occur in the morning generate long-term effects that increase social bonding behaviors within groups later in the evening, such as allopreening and roosting (Radford and Fawcett 2014). Experience of same-sex contests in juvenile female burying beetles (*Nicrophorus vespilloides*) increases reproductive output later in life, possibly as a result of increased post-hatching brood care, regardless of the outcome of the contest (Pilakouta et al. 2016). Learning from social experience is a related, and widespread, example of how the phenotypic impact of the social environment can be temporally separated from individual encounters. Learned mate preferences are now commonly studied (Dukas 2005; Verzijden et al. 2012), and when such changes in female mating behavior involve IGEs, their impact on sexual selection and diversification can be significant (Bailey and Moore 2012).

Time-delays between when a social interaction occurs and a focal individual's phenotype changes will affect the phenotypic trait values that are ultimately available to the action of selection. Time-courses of IGEs can be linked to underlying physiological and neuronal processes that shape trait expression, and vary widely. IGEs can influence "slow-changing state variables," such as metabolism-dependent body growth, in addition to "fast-changing state variables," such as near-instantaneous behavioral adjustment during an agonistic encounter (Niemiälä and Santostefano 2015). Examples of both are readily found in the literature. For example, IGEs on growth in pigs arising from behavioral phenotypes such as aggressive biting are not only documented, but have been successfully selected in artificial breeding programs (Camerlink et al. 2013, 2014). In contrast, isogenic focal *Drosophila melanogaster* males vary in how much they physically tap interacting partners of different genotypes with their prothoracic legs during bouts of interaction lasting only minutes, a behavior that might reflect gustatory sampling or aggression (Bailey and Hoskins 2014). Not only the timing of socially plastic responses underlying IGEs, but when during life any fitness effects of those changes are manifested, will ultimately impact evolutionary dynamics shaping behavior (Schneider et al. 2017). If the phenotypic effects of IGEs are invisible to selection, they will not contribute to evolutionary dynamics.

IGEs IN BEHAVIORAL ECOLOGY RESEARCH

Improving optimality predictions using IGEs

Adopting an interacting phenotype approach would be merely a curiosity if it provided no insights over approaches based on the phenotypic gambit. Optimality has provided a useful framework for making predictions in experimental animal behavior research programs. Understanding causes of variation is a cornerstone of behavioral ecology, taught in undergraduate courses and featured in canonical texts (Davies et al. 2012). Yet optimality assumes a population has reached an evolutionarily stable state. This represents a limitation for behavior that has been suggested to reflect ignorance of mechanisms such as genetics (Moore and Boake 1994). Animal behaviors can often appear counter-intuitive or non-adaptive at first blush (Bailey 2013), and the extent to which dissecting the underlying causal mechanisms of behavior can enlighten us about its ultimate causes represents a persistent tension within the field (Tinbergen 1963; Mayr 1961; Laland et al. 2011). The theoretical framework of IGEs provides one way of reconciling optimality predictions and variable behavior. In the remaining sections, we describe how IGEs have been detected in behavioral studies to date, what insights have been gained, and why behavioral ecology studies can benefit from including IGEs in the toolkit of "proximate causes" of behavioral variation. We finish by proposing that behavioral ecologists can use IGEs as a powerful conceptual tool to inform, with quantitative predictions and data, the debate about whether behavior is a unique sort of trait with emergent properties making it difficult to characterize genetically, but at the same time lending it a special role in evolution.

Theoretical insight into the influence of IGEs on behavior

The role of the social environment in shaping behavior has been a dominant theme in behavioral ecology studies, and there is a growing interest in incorporating mechanisms into such studies (Hoffman et al. 2014), including IGEs. The question is whether considering a given behavior as susceptible to genes expressed in social partners lends insight to our understanding of the forces that cause that behavior. Drown and Wade (2014) pitted genotypes with varying degrees of sensitivity to the social environment against one another in a series of quantitative genetic models, to assess the contribution of heritable variation in the environment on evolutionary rates. They found that heritable components of the environment, IGEs, can generate runaway evolution when they become linked with genetic variants that control responses to that social environment. Rapid coevolutionary dynamics are a specific consequence of responses to genes in the social environment, rather than responses to abiotic environments.

Rapid evolution can become runaway. Bailey and Moore (2012) examined the evolution of sexual signals and mating preferences and found that a key determinant of whether IGEs accelerate or retard sexual trait elaboration is the sign and magnitude of the interaction coefficient ψ , which alters the influence of trait-preference genetic covariance during runaway coevolution. Accumulation of genetic covariances between sexual traits and preferences are a fundamental property of Fisher's original model of sexual selection (Fisher 1915, 1958), but incorporating IGEs counterintuitively suggested that trait-preference covariances can be smaller than expected while still allowing runaway to occur. This finding may help to reconcile a pervasive lack of evidence for

expected trait/preference genetic covariances in empirical studies (Greenfield et al. 2014). IGEs have also been modeled in sexual conflict scenarios, and when strong, they are predicted to stimulate rapid evolutionary proliferation of adaptations and counter-adaptations above standard predicted rates (Moore and Pizzari 2005).

Evolutionary dynamics that can arise through IGEs address 2 issues affecting commonly studied traits in behavioral ecology such as ornaments, mate preferences and armaments. The first is that IGEs might provide an evolutionary genetic mechanism for the prediction that such traits are labile in varying social environments, which has been confirmed in numerous phenotypic studies on learning and mating behavior (Dukas 2005; Kozak and Boughman 2008, 2009; Bailey et al. 2010; Bailey 2011; Rebar et al. 2011, 2016; Auld et al. 2016; Rebar and Rodríguez 2016). Thus, IGEs allow the flexibility we see in social behavior to be consistent with standard evolutionary theory. The second is that they refine our expectations of what is an optimal behavior in circumstances where IGEs are expected, enabling a better explanation of seemingly perplexing traits. Empirical research is now beginning to put these ideas to the test.

Empirical evidence for IGEs in behavioral ecology research

Explicitly considering IGEs in behavioral studies provides a more accurate understanding of what causes behavioral variation, and in some cases can fundamentally change our interpretation of those causes. IGEs for sexual traits such as signals and female mating preferences have now been documented in several invertebrate systems, and in a smaller number of studies, have been demonstrated to evolve. In *Drosophila melanogaster*, IGEs exerted through social interactions alter the composition of sexually selected male cuticular hydrocarbons (CHCs) (Kent et al. 2008). In the related species *D. serrata*, the genotype of interacting females has been found to explain nearly a fifth of the variance in male CHC profiles (Petfield et al. 2005), and the expression of 2 methyl-branched alkanes important for sexual signaling in males can be artificially evolved under different female social environments (Chenoweth et al. 2010). In one strain of the lesser waxmoth *Achroia grisella*, male body mass and the pulse-pair rate and peak amplitude of ultrasonic advertisement songs were found to be affected by IGEs (Danielson-François et al. 2009). In different populations of the field cricket *Teleogryllus oceanicus*, female choosiness in mating trials is affected differently by the previous experience of singing males or silence, suggesting population-level variation in the interaction coefficient Ψ for these traits (Bailey and Zuk 2012).

Researchers have also quantified IGEs on traits that mediate sexual conflict (e.g., Signor et al. 2017). In the hermaphroditic flatworm *Macrostomum lignano*, there is striking heterogeneity in the presence, strength and direction of IGEs on multiple morphological and behavioral traits with expected roles in sexual conflict, such as gonad size and copulation latencies (Marie-Orleach et al. 2017). *Macrostomum lignano* performs an intriguing behavior after copulation in which individuals apply their pharynx on top of their own sperm storage organ and appear to suck it (Schärer et al. 2004; Vizoso et al. 2010). This behavior is facultative and thought to be involved in removing from storage some components of the recently received ejaculate. Optimality models not considering IGEs would predict that sperm recipients suck only when it is beneficial to them, for example, when they do not need extra sperm for fertilization. However, the propensity to suck depends to some extent on the genetics of the sperm donor, which opens the possibility for

manipulation of the partner's suck behavior through prostate gland secretions (Marie-Orleach et al. 2013; Marie-Orleach et al. 2017). Thus, this behavior would appear counterintuitive, or nonoptimal, if IGEs are not considered. Other examples exist in the field of animal breeding, in which programs considering IGEs have been shown to improve the response of selection for various traits of interest to breeders (e.g., growth rates in pigs, or plumage condition in laying hens) (Camerlink et al. 2013, 2015; Brinker et al. 2014). In Table 1, we provide additional examples illustrating how considering IGEs can modify our interpretations of a behavior's causes, and reveal unsuspected evolutionary forces influencing their expression.

In laboratory mice, a cross-fostering experiment demonstrated that offspring genotype influences maternal care behaviors, providing a genetic mechanism mediating the evolution of parent-offspring conflict (Ashbrook et al. 2015). As these were lab mice, the researchers mapped genomic loci that might play a role in mediating those effects, providing clues about causal offspring behaviors, such as solicitation, to which mothers responded. In *D. melanogaster*, the genotype of male mating partners exerts a significant impact on copulation duration, illustrating that it is not solely under female control (Edward et al. 2014). Nevertheless, other female traits that would be expected to be susceptible to sexual conflict dynamics such as egg production showed no IGEs (Edward et al. 2014). Another *D. melanogaster* study recovered a significant effect of male partner identity on female fecundity, consistent with a male IGE affecting female fitness components (Fennant et al. 2014). Male IGEs affecting female fecundity appear to be exerted through male mitonuclear epistasis in seed beetles (*Callosobruchus maculatus*), suggesting a complex interplay between organelle-specific IGEs and sexual conflict (Immonen et al. 2016).

Nonsexual social behaviors are also impacted by IGEs. Normally the purview of inclusive fitness theory and kin selection, behaviors critical to the functioning of animal societies are increasingly being studied from the viewpoint of interacting phenotypes and IGEs (Linksvayer 2006; Linksvayer 2015; Linksvayer and Wade 2016). In *Pogonomyrmex californicus*, a harvester ant, variation in the social composition of founding groups of queens in cooperative colonies determines behavioral outcomes in aggression and brood care phenotypes (Clark and Fewell 2013). IGEs have been documented across a range of additional social traits, including paternal care (Head et al. 2012), social dominance (Moore et al. 2002; Wilson et al. 2011), agonistic encounters (Wilson et al. 2009; Santostefano et al. 2016), group antipredator behavior (Bleakley et al. 2009; Edenbrow et al. 2017), and breeding date in birds (Germain et al. 2016). In the mosquitofish *Gambusia holbrooki*, direct genetic effects (DGEs) influence the number of social partners that males of different color morphs encounter, illustrating how DGEs and IGEs can covary (Kraft et al. 2016), a critical parameter influencing evolutionary dynamics (Bijma 2014).

IGEs are also relevant to the expression of behaviors within interspecific and multitrophic interactions. Interspecific IGEs can have a wider impact on the evolution of community assemblages and ecosystem functioning (Genung et al. 2013a, 2013b). For example, the genotype of a parasitoid wasp *Aphidius ervi* influences whether infected aphids (*Acyrtosiphon pisum*) remain on or abandon their host plant, and dictate the final location of death of aphids who choose to remain (Khudr et al. 2013). Male treehoppers (*Enchenopa binotata*) use substrate-borne vibratory communication as a sexual signal, and the genotypes of plants used as vibratory substrates affects both the expression of male signals and female mating decisions (Rebar and Rodríguez 2014a, 2014b). Genotypic variation among substrate plants also mediates the phenotypic covariance of the treehoppers' sexual trait and preference (Rebar and Rodríguez 2015).

Table 1

Examples of behavioral traits for which considering IGEs has changed inference about the causes of variation, including maternal care, social behaviors, sexual selection, and animal breeding examples from recent studies

Trait description	Interpretations when IGEs are omitted	Interpretations when IGEs are considered
Maternal care in laboratory mice (<i>Mus musculus</i>).	Maternal care is only determined by the mother's own genes, and her (nongenetic) environmental conditions. Mothers invest optimally in maternal care to optimize their inclusive fitness.	The offspring genetics also influences maternal care, which enables optimal coadaptation between the levels of maternal care and offspring solicitation (Ashbrook et al. 2015).
Maternal care in the European earwig, <i>Forficula auricularia</i> .	Maternal care is only determined by the mother's own genes, and her (nongenetic) environmental conditions. Mothers invest optimally in maternal care to optimize their inclusive fitness.	Investment in maternal care is also influenced by the genetics of the offspring and the father. This implies that maternal care is governed by mutualistic and antagonistic coevolution between the mother, the father, and their offspring (Meunier and Kölliker 2012).
Antipredator behavior in guppies, <i>Poecilia reticulata</i> .	Antipredator behavior expressed only at the benefits of the individual expressing it. The evolution of social behavior and cooperation among unrelated social partners is paradoxical.	The genetics of social partners influence antipredator behavior, which facilitate the evolution of antipredator behavior, cooperation, and social behavior (Bleakley and Brodie III 2009).
Song produced by the male lesser waxmoth, <i>Achroia grisella</i> , involved in female mate choice	The male song is only determined by the male's own genes, and his (nongenetic) environmental conditions. Female mate choice should rapidly erode the genetic variation in song production (The Lek paradox).	The male song is also modulated by the genetics of male social partners, which contributes to maintain genetic variation in song production (Danielson-François et al. 2009).
The suck behavior facultatively expressed after copulation by the hermaphroditic flatworm, <i>Macrostomum lignano</i> , during which worms apply their pharynx on top of their own sperm storage organ and appear to suck.	Worms suck when it is beneficial to them, e.g., no need of extra sperm for egg fertilization, use ejaculate as food resource, cryptic female choice.	The suck behavior is also the target of manipulation by the mating partners at their own benefits, e.g., use sperm for egg fertilization (Marie-Orleach et al. 2013, 2017).
Growth rate in domestic pigs, <i>Sus scrofa</i> , used in breeding programs.	Growth rate is only determined by the pig's own genes and its (nongenetic) environmental conditions. Artificial selection on high growth rate should produce pigs that grow faster.	Pig growth rate is also influenced by social interactions with their penmates, such as aggressive and biting behaviors (Camerlink et al. 2015). Breeding programs accounting for IGEs provide better outcomes (Muir 2005).
Male leg tapping in the fruit fly <i>Drosophila melanogaster</i> , in which the prothoracic leg is extended and contacts the cuticle of another individual.	Tapping behavior is controlled by focal males and is expressed in the context of chemosensory sampling or aggressive interactions.	Expression of tapping behavior depends on elicitation or opportunity controlled by the genotype of interacting partners. A combined trait-based and variance partitioning approach identified a behavioral trait, the startle response, as a possible mediator of this IGE (Bailey and Hoskins 2014).

TESTING BEHAVIOR'S "SPECIAL ROLE" IN EVOLUTION

Behavioral susceptibility to IGEs

Until now, we have documented how IGEs can affect the expression of commonly studied behaviors, helping to explain unexplained variation. It is also important to consider how behavioral ecology studies can inform the broader evolutionary implications of IGEs. Are behaviors especially prone to responding to IGEs in a way that accelerates, decelerates or otherwise modifies evolutionary trajectories? Over the past several decades, the field of behavioral ecology has shown how exquisitely sensitive animal behavior is to the social environment, even in species that typically spend their lives in asocial states. In addition, there is increasing evidence that IGEs affect many behaviors, and thus processes that behavioral ecologists study. But is behavior unique in this respect? Some would argue yes: part of the call for an extended evolutionary synthesis relies on the intuition that the extreme responsiveness of behavior to the environment and unexpectedly rapid evolutionary change requires a new evolutionary explanation (Laland et al. 2011, 2014, 2015). However, IGEs and interacting phenotype theory provide an explanation for extreme plasticity and variability, for evolutionary

change without DGEs, and for rapid evolution of traits that are sensitive to social environments, that is fully consistent with standard evolutionary theory.

What proportion of V_P is $V_{E(\text{social})}$?

The starting point for predicting which traits in focal individuals are most likely to contribute to evolutionary dynamics through IGEs—and testing whether behavioral traits are systematically over-represented in this category—is to establish whether any of the traits in question respond to variation in the social environment. If so, then this is an interacting phenotype. The insight that behavior can be affected by social interactions may be obvious, but traits such as morphology also respond to variable social environments, often through density-dependent or maternal effects. Second, we can ask whether genetic heterogeneity among individuals affects the contributions of the social environment to phenotypes. If so, then IGEs exist. The relative importance of IGEs can be measured against the contributions of DGEs. Studies that have quantified IGEs using either variance partitioning or trait-based approaches on multiple phenotypes have tended to find heterogeneity across assayed traits in their responsiveness to genes in the social environment.

For example, ca. 18% of heritable variation in growth rate in the flour beetle *Tribolium castaneum* was influenced by IGEs, while no such influence was documented for other life-history traits in the same study (Ellen et al. 2016). A trait-based analysis of 5 antipredator and social behaviors in the guppy *Poecilia reticulata* found evidence for reciprocal IGEs on all traits, but only a limited number of nonreciprocal IGEs, and their directions and magnitudes varied (Bleakley et al. 2009). In the latter study, the extent of schooling behavior in focal individuals was negatively related to the tendency of social partners to remain near a model, whereas the amount of time a focal individual spent in proximity was positively related to agitation behavior in interacting partners.

The final requirement for testing whether the flexibility of behavior makes it particularly susceptible to IGEs is to systematically compare different types of traits. The variance-partitioning approach (Box 2) can quantify the amount of phenotypic variance

BOX 2. BEHAVIOR'S SPECIAL ROLE IN EVOLUTION: ARE BEHAVIORAL TRAITS ESPECIALLY SUSCEPTIBLE TO IGEs?

Flexibility is a defining feature of behavior. While multifactorial causes, reversibility and context-dependence can make behavioral traits less repeatable, posing technical challenges to their accurate quantification, the same characteristics have also been argued to confer special properties to behaviors that other traits do not share. For example, unusually high plasticity can be advantageous in situations where quick or reversible phenotypic responses are required, such as sexual selection, sexual conflict, signaling, or dominance interactions (Mayr 1974; West-Eberhard 1989, 2003). However, there is unresolved debate around the ultimate consequences of this sort of phenotypic lability. A simplified version of the question underpinning this debate is whether phenotypic flexibility of behavior (i.e., a tendency to high plasticity) causes it to have a special role in processes such as those mentioned above, and in evolutionary change more generally. If behavior is thus set apart from morphological, life history or physiological traits, studies seeking to explain the causes or consequences of variation in animals will benefit from a better understanding of phenotypic expectations for behavioral traits. This can be informed by quantifying and comparing the influence of IGEs. Here we outline a method to do so.

It would be profitable to test the prediction that IGEs are more common and of greater magnitude for behavioral traits, compared with other types of traits. If supported, this would provide evidence that IGEs represent at least one distinct, quantifiable mechanism underlying a unique role for behavior in determining patterns of organismal diversity more generally. This is analogous to the approach adopted by Mousseau and Roff (1987) comparing heritabilities of life-history traits, morphological traits, behavioral traits and physiological traits. The idea is to partition sources of phenotypic variation into direct and indirect genetic influences, the former arising from individual actors and the latter from genes expressed by other individuals with whom they socially interact.

There are 2 ways to do this (McGlathlin and Brodie 2009). If the specific traits and their influences are known, a trait-based approach is the most powerful as it allows a consideration of the extent that the social environment matters for each trait (estimated using the interaction coefficient ψ , cf.

BOX 2. Continued

Moore et al. 1997; see Box 1). However, researchers often do not know ahead of time the traits that should be measured or that are having an influence; we often know that the social environment matters, but no more than that (Bailey and Hoskins 2014). Under such conditions a variance-partitioning approach is informative. Extensive mathematical treatments of IGEs have been published elsewhere, and interested readers are encouraged to consult these resources to learn more about the practicalities of experimental and breeding designs (e.g., Moore et al. 1997; Bijma 2010, 2014; Bleakley et al. 2009; McGlathlin and Brodie 2009). Here, we focus on parameters of key interest that are accessible to researchers for quantifying the existence, prevalence, magnitude, and potential consequences of IGEs.

Considering a finite population of conspecifics, a variance-partitioning can be described with mathematical expressions. Following the derivations in Bijma (2014), we can describe how the total phenotypic variance, σ_p^2 , is composed of variance from DGEs caused by genes expressed within individuals that affect their own phenotypic trait values, $\sigma_{a_D}^2$ (subscripts a denoting additive genetic effects and D for direct effects), variance arising from genes expressed in interacting social partners (IGEs), $\sigma_{a_S}^2$ (subscript S showing that the genetic variance arises from social interactions) scaled by the number of nonfocal interacting partners ($n - 1$), plus all other sources of nonheritable variation, ϵ_i :

$$\sigma_p^2 = \sigma_{a_D}^2 + (n-1)\sigma_{a_S}^2 + \epsilon_i \quad \text{Eqn 2.1}$$

Throughout this explanation, variance terms representing DGEs are colored in blue, while those representing IGEs are colored red. For our purposes, we are only interested in genetic sources of phenotypic variation, whether arising directly within focal individuals ($\sigma_{a_D}^2$), or from genes expressed in interacting social partners ($\sigma_{a_S}^2$). The importance of direct and indirect genetic effects can be assessed by examining their contribution to the *evolutionary potential* of a population of individuals. This is equivalent to the total variance in the breeding value (cf. Bijma 2014), which is comprised of additive effects a_D and a_S :

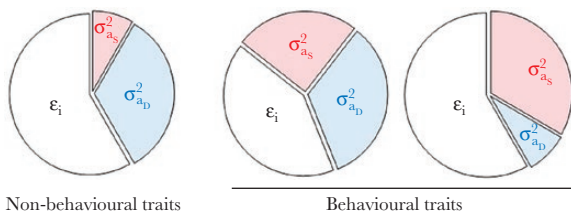
$$\text{evolutionary potential} \sim \sigma_{a_D}^2 + 2(n-1)\sigma_{a_{(D,S)}}^2 + (n-1)^2\sigma_{a_S}^2 \quad \text{Eqn 2.2}$$

Evolutionary potential describes the possible response to selection. If selection is assumed to be constant, the expression above illustrates how IGEs can affect the ultimate evolutionary outcome of traits. The middle term in purple represents covariance between direct and indirect genetic effects. Its importance is beginning to be investigated in empirical behavioral studies, and on a functional level this can be thought of as the degree to which the trait that responds to social environments in a focal individual also reflects the social environment that the focal individual provides to others – strong, positively associated effects will tend to enhance evolutionary potential, while opposing effects will impede the response to selection.

If IGEs affect behavior disproportionately, then this leads to the prediction that IGEs should be detected more frequently for behavioral traits than nonbehavioral traits, provided traits are surveyed in an unbiased manner and measured on a standardized scale. In addition, the approach described above

BOX 2. Continued

can be used to quantify magnitudes of components and compare them among trait types. To make this comparison, we advocate calculating evolvability, which is the coefficient of variation standardized by the mean. This approach allows comparison of the relative importance of IGEs and DGEs under standard quantitative genetic assumptions, and is similar to that used by Baud et al. (2017) in controlled experiments with laboratory mice. A caveat is that transforming phenotypic values prior to calculating genetic variances, as was done using a Box-Cox power transformation to satisfy model assumption in Baud et al. (2017), can complicate subsequent comparison of evolvabilities (Garcia-Gonzalez et al. 2012). Thus, to enable inference about both the relative influence of IGEs, and to compare differences in absolute evolutionary potential contributed by IGEs across traits or organisms, we advocate comparing mean-standardized variances (Hansen et al. 2011; Garcia-Gonzalez et al. 2012). The figure below shows a comparison of hypothetical variance components for different traits, in which we have arbitrarily set the total phenotypic variances to be equal for purposes of illustration.



Consider a moderately heritable trait, where approximately 30% of the total variance reflects the contributions (or variance associated with) additive genetic effects. If it is non-behavioral, the prediction is that any variance component describing IGEs will be relatively small (left). If behavioral traits are more susceptible to IGEs, indirect genetic variance may represent a greater proportion of the overall environmental variance (middle), in which case nonheritable effects ϵ_i are diminished. However, IGEs may also represent a relatively larger fraction of genetic variance overall even if nonheritable effects remain constant (right). Comparing the relative proportions of phenotypic variance explained by DGEs versus IGEs among different traits addresses the question: “are IGEs more important than DGEs for behavior, but not other traits?”, but absolute, mean-standardized variances can also be compared to ask “what is the absolute importance of IGEs to the evolvability of different trait types, regardless of DGEs?”

A finding that behavior is more affected by IGEs would support its hypothesized distinctive role in evolution, and lend insight into its expression in circumstances that interest behavioral ecologists. However, failure to establish a difference between behavioral and nonbehavioral traits would be interesting as well. Such an outcome would not negate the proposition that behavior can be involved in unique evolutionary dynamics as a result of its lability, for it may be that such dynamics involve only a specific, restricted set of

BOX 2. Continued

behaviors. However, failing to generally distinguish behavioral traits versus other types of traits based on an important genetic cause, IGEs, would stimulate more general reflection on the distinctive biological properties of *behavior* as a unitary phenomenon, and perhaps return us to ideas developed during the origins of modern ethology, animal behavior and behavioral ecology, encapsulated by Lorenz’s (1941) famous observation in a comparative study of birds that “[t]he few morphological characters distributed in the table are intended to show how similar their distribution is in many cases to that of the *innate behavior patterns*.”

associated with different sources using standard quantitative genetic approaches. Environmental influences on a given trait’s expression can be subdivided into effects of the physical environment and those of the social environment (Moore et al. 1997; Bijma 2014). Standardizing trait values is necessary if traits are measured in units, but there are no restrictions on the types of traits that can be measured. The key question is whether the partitioning differs for behavioral traits versus other traits such as morphology, life history, or physiological attributes.

Nested hypotheses can be used to interrogate this question: can we first reject the null hypothesis that there are no environmental influences on trait expression (i.e., plasticity—this requires testing in multiple environments)? Next, can we reject the null hypothesis that there are no effects of the social environment on trait expression (i.e., interacting phenotypes—this requires testing over variable social environments)? If an interacting phenotype exists, can we reject the null hypothesis that there are no IGEs arising from that social environment effect (IGEs—this requires pedigrees or breeding designs to identify genetic effects)? In the final analysis, a proportion of explained variance can be assigned at each level of this hierarchical model. The process can be iterated for a panel of different traits, marrying the ability of the trait-based interacting phenotype approach to interrogate specific phenotypes with the ability of the variance partitioning approach to estimate relative contributions of any IGEs. An important consideration is to avoid biasing the outcome when selecting such a panel of traits; for example, by focusing on behaviors known to be particularly labile.

Partitioning variance for a panel of randomly-chosen traits can seem a daunting task, but a recent study examining the effects of IGEs on health and disease factors in lab mice, *Mus musculus*, is one of the first tests using such an approach and provides a guide forward. Baud et al. (2017) assayed over 100 phenotypes related to health and disease after housing mice of different genotypes together. In their first experiment using 2 inbred lines of mice, the authors detected IGEs in 11 out of 50 phenotypes assayed. In a separate experiment with an outbred population, the authors detected IGEs in 43 out of 117 traits assayed, and in 8 of those 43, IGEs explained a greater proportion of variance than DGEs (Baud et al. 2017). The design of the experiment did not enable a conclusion regarding the likelihood of behavioral traits experiencing IGEs versus other sorts of traits, owing to the nonrandom selection of assayed phenotypes.

IGEs in more than one phenotype allow estimates of the multivariate matrix of interaction coefficients, Ψ (e.g., Bleakley and Brodie III 2009; Marie-Orleach et al. 2017), and identification of candidate interacting phenotypes underlying “hidden” IGEs by comparing

values of ψ across multiple traits (Bailey and Hoskins 2014). It might be similarly possible to test hypotheses about the role of behavior in evolution in a more trait-aware fashion, using comparisons of ψ . However, the field still lacks a systematic comparison of amounts of variance explained across different categories of traits. Such studies could use panels of inbred lines (e.g., Fuller and Hahn 1976; Bailey and Hoskins 2014; Baud et al. 2017), or pedigreed populations (e.g., Wilson et al. 2009; Germain et al. 2016). Experimental evolution approaches would also allow an assessment of how IGEs versus DGEs contribute to selection responses, which could be used to test the evolutionary potential of different types of traits. Work that explicitly tests whether behavioral traits are more often subjected to IGEs would inform debate in behavioral ecology over the role of behavior as a phenotypic “arena” in which sexual selection, conflict, and dominance are enacted in animals, and ultimately address the question of whether IGEs exerted through behavior are particularly important—or not—in leading evolutionary change.

SUMMARY AND RECOMMENDATIONS

Accounting for the influence of genes on the social environment can improve optimality predictions that might be otherwise thwarted by the complex, flexible, multivariate nature of most behaviors (Table 1). Just as Hamilton’s Rule provided a gene-centric impetus for better optimality predictions about altruism, kin selection, animal societies, group selection, etc., we suggest that considering IGEs in the social environments of animals, broadening social to include any interaction, will facilitate a better understanding of the costs and benefits of behavior that appears unusual, improbable, or inexplicable. Behavioral ecologists are just beginning to use the framework of IGEs to test how genes expressed in interacting social partners affect expression of behaviors in a variety of contexts, but models suggest that IGEs should matter in sexual selection, sexual conflict, the maintenance of dominance hierarchies, and evolution of sociality. IGEs can lead to quantifiably more rapid responses to selection. As we have reviewed, these efforts resolve mismatches between predicted and observed genetic architectures of secondary sexual traits and mating preferences, informing the paradox of the lek, and providing quantitative tests about the number and nature of sexually antagonistic adaptations and counter-adaptations. The nascent empirical literature on IGEs in behavioral ecology indicates that formulating hypotheses and predictions that incorporate genetic effects in interacting social partners can similarly enhance the abilities of behavioral ecologists to test causes of behavioral variation.

The field of behavioral ecology has an opportunity to capitalize on a well-developed quantitative genetic framework to inform a longstanding debate about the unusual role of behavior in evolution. Are behavioral traits more susceptible to IGEs compared with morphology, life history, and physiology? Depending on the answer to that question, systematically examining whether different types of interacting behavioral phenotypes are more influenced by IGEs than others will further clarify how and when behavior might cause unique evolutionary effects. Susceptibility to IGEs may drive distinctive evolutionary dynamics in behaviors involved in, for example, conflict, cooperation, or reproductive interactions. We consider it to be an intriguing possibility that behavior might play a unique role in “leading evolution,” but despite over a century of intense interest, this debate is unresolved. IGEs provide behavioral ecologists with a means for putting this idea to the test with falsifiable hypotheses, quantitative predictions, and hard data.

FUNDING

The authors gratefully acknowledge funding to NWB from the Natural Environment Research Council (NE/I027800/1), to L.M.-O. from the Swiss National Science Foundation (P2BSP3_158842), and to A.J.M. from the National Science Foundation (IOS-1326900).

Editor-in-Chief: Leigh Simmons

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