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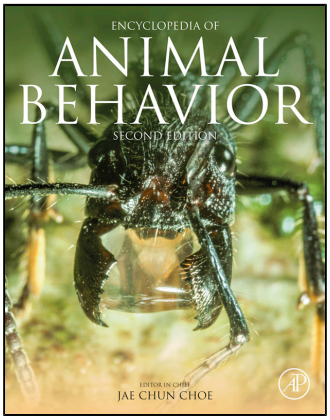

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Indirect Genetic Effects

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Glossary

Indirect genetic effects (IGEs) Genetic variation in the effect that some individuals have on the phenotype of other individuals with whom they interact.
Interacting phenotypes Traits influenced by, or depedent on, interactions with other individuals.
Interaction coefficient ψ, Regression coefficient describing the effect of interacting partners' phenotypes on focal individuals' phenotypes, indicating the strength and direction of IGEs.
Phenotypic plasticity A genotype's change in phenotypic trait value under different environmental conditions.
Social selection Fitness variation arising from social interactions.

Abstract

The concept of Indirect Genetic Effects (IGEs) captures the insight that trait expression often receives inputs not only from the genotype of the bearer of the trait (the focal individual), but also from the phenotype of other individuals with whom the focal individual interacts. This concept is intuitive if we consider behavior: how an animal acts is often influenced to some degree by how other individuals around it behave. Consequently, an animal's behavior is not only shaped by inputs from its own genotype, but also from the genotypes of those other individuals. The variety of traits that exhibit this architecture is surprisingly large, including not only many behaviors but also morphological and life history traits, and the relevant inputs can arise not only from behavioral interactions but also from ecological relationships. Taking into account this broader view of trait architecture brings insight into how phenotypic and genetic evolution proceed.

Keywords

Behavioral flexibility; Causes of variation; Experience-mediated plasticity; Interacting phenotypes; Interaction coefficient; Phenotypic plasticity; Psi; Quantitative genetics; Runaway; Sexual selection; Social selection

Introduction

To study animal behavior is to see one of the most abstruse concepts in evolutionary biology come to life. The concept: there is a type of trait that varies according to: (i) the bearer's own genotype and environment, and also according to: (ii) the genotype and environment of the individuals with whom the bearer interacts (Moore *et al.*, 1997; Wolf *et al.*, 1998; Bailey *et al.*, 2018). Such traits are termed interacting phenotypes and are found across a diversity of contexts. A useful framework for understanding and studying interacting phenotypes is to consider what causes their variation. Indirect genetic effects (IGEs) describe genetic inputs into the expression of any given individual's traits that arise from its interactions with other individuals. This term differentiates such components of variation from the bearer's own direct genetic inputs (Direct Genetic Effects, DGEs) into trait expression, and allows a useful expansion of methods to study the complex and interrelated evolutionary causes and consequences of interactions between individuals.

Animal behavior offers prime examples of interacting phenotypes, because behaviors are often an emergent property of an individual's interactions with others. Whether an animal is communicative or secretive, collaborative or competitive, amorous or aggressive, and how it goes about satisfying its needs, is at least in part (and often wholly) a function of who else is around and what they are doing. Students of animal behavior can no doubt supply their own examples. One of our favorites: In many spiders, a female will approach and solicit a mating from a male she finds attractive but attack and eat a male she finds unattractive; and the extent to which she signals responsiveness will vary according to just how attractive the acceptable male is (Sullivan-Beckers and Hebets, 2014). Interacting phenotypes span a broad range of contexts, from signaling and communication, to parental care, aggression and dominance, cooperation, and mating; and they occur in a diversity of taxa. Social behavior is a defining feature of animal life, and interacting phenotypes are therefore widespread.

Phenotypes that vary according to the above direct and indirect genetic influences also occur beyond behavior and beyond interactions with conspecifics. A large fraction of the phenotypes of most organisms vary according to the social and developmental

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environment in which they are expressed (West-Eberhard, 2003, 2005; Ghalambor *et al.*, 2015). And those environments are in many cases biotic; that is to say, they consist of other organisms. Parasites and parasitoids, herbivores and symbionts – all sorts of organisms spend at least some part of their lives on (or in) their hosts, and many interact with the extended phenotypes of other organisms (Bailey, 2012). For example, invertebrate ectoparasites of birds breed in bird nests, and their presence in the constructed environment made by birds can drive onward adaptations in the birds themselves (López-Rull and Macías-Garcia, 2015). In these cases, the environment itself has genetic components of variation that may influence the expression of the phenotypes of the individuals that live in it: the environment contains genes (Wolf, 2003). For the case where environments consist of conspecific individuals that may interbreed, these genes and their effects on the traits of other (IGEs) can cause interesting and extreme evolutionary dynamics through evolutionary feedback mechanisms which we discuss below.

The above means that the genetic and developmental architecture of many traits is intricate, in two main dimensions. First, understanding how variants arise, and how they respond to selection, requires accounting not only for the direct components of genetic and environmental variation but also for the indirect components. Second, the nature of selection on these traits is modified in curious but powerful ways by the phenotypes of the individuals around them.

Direct and Indirect Components of Trait Variation

The expression of a trait receives direct inputs from the genotype and environment of the bearer (Lynch and Walsh, 1998; West-Eberhard, 2003). The expression of that same trait also receives inputs from the conspecific and heterospecific individuals with whom it interacts, as well as from other components of its biotic environment. Importantly, those inputs also have genetic and environmental components of variation.

We sketch these inputs out in **Fig. 1**. Consider the top individual in any one of the boxes in the figure. We refer to that individual as the focal individual (but note that the same dynamics may pertain to the other individual in the interaction, and, in fact, reciprocally). The phenotype of the focal individual receives direct inputs from its genotype (additive genetic effects) and its environment (a, e, respectively). When dealing with interactions between conspecifics, these genetic inputs are IGEs (**Fig. 1**; blue arrows and box). But, as we note above, such effects can also arise from interactions with heterospecifics, in which case they are termed Interspecific Indirect Genetic Effects (IIGEs) (**Fig. 1**; pink arrows and box), and these may even be cross-trophic (**Fig. 1**; green arrows and box). In other words, the interactions to which we refer here may range from the social to the ecological. Hereafter, we use the term IGEs broadly to include all of the above categories, and we use IIGEs and cross-trophic IIGEs to refer specifically to effects that arise from interactions between species.

There are examples of indirect genetic effects for all sorts of traits at all three levels. Within species, IGEs have been found to influence various kinds of behavior and to be taxonomically widely distributed. Examples include IGEs influencing variation in locomotion behavior and chemical signals in fruit flies (Petfield *et al.*, 2005; Kent *et al.*, 2008; Chenoweth *et al.*, 2010; Signor *et al.*, 2017); body mass and male acoustic signals in wax moths (Danielson-François *et al.*, 2009); testis and seminal vesicle size and sperm-removal behavior in flatworms (Marie-Orleach *et al.*, 2017); mate preferences for vibrational signals in treehoppers (Rebar and Rodríguez, 2013); antipredator behavior in guppies (Bleakley and Brodie, 2009); egg-laying date in gulls (Teplitsky *et al.*, 2010); feeding intake and growth rate in fish, pigs, and quail (Wade *et al.*, 2010); maternal provisioning and offspring solicitation in burrowing bugs (Agrawal *et al.*, 2001); exploratory boldness in crickets (Rudin *et al.*, 2018) and educational attainment in humans (Kong *et al.*, 2018). There is also an example of IGEs in plants, influencing the growth characteristics of neighboring individuals Mutic and Wolf, 2007.

There have been fewer studies of IIGEs, but even here there are interesting examples. Bottom-up cross-trophic IIGEs have been documented on advertisement signals and mate preferences, arising from genetic variation in the host plants on which plant-feeding insects live (Rebar and Rodríguez, 2014a,b, 2015). Furthermore, this study found surprisingly strong signal-preference phenotypic covariance arising from these IIGEs, which lends support to the hypothesis that such effects can generate runaway sexual selection and promote speciation via rapid divergence in reproductively isolating traits (Bailey and Moore, 2012), perhaps more powerfully than runaways involving direct signal-preference genetic covariance (Greenfield *et al.*, 2014; but see Fowler-Finn and Rodríguez, 2016; Sharma *et al.*, 2016). There is also an example of top-down cross-trophic IIGEs, with inputs from parasitoid wasps influencing their aphid hosts' positioning and remaining on the host plant (Khudr *et al.*, 2013).

The phenotypic change induced by the social environment can be thought of as a phenotypically plastic response to a key element of that social environment: from this perspective, trait expression of the same focal genotype can change as a result of interacting with different social partners. The coefficient ψ describes how the environment contributed by the value of one specific trait, expressed by an interacting individual, translates into changed expression of a trait in the focal individual. ψ is useful for understanding how IGEs impact behavior, because it indicates the direction and magnitude of change (i.e., plasticity) in the focal individual's phenotype due to its interactions with social partners. Where the traits under consideration are different for the two partners, (for example a contact pheromone in one individual and level of aggressiveness in another), these can be indicated by subscripting: $\psi_{a,b}$. Interactions might be reciprocal such that the expression of trait a affects that of trait b and vice-versa, and they might be reciprocal and involve the same trait (Moore *et al.*, 1997). A common example of the latter occurs during escalating aggressive encounters between interacting individuals (Wilson *et al.*, 2009). Larger numbers of traits can be considered in a multivariate context by defining, estimating and modeling a matrix of interaction coefficients, $\boldsymbol{\Psi}$, so there are analytical and empirical

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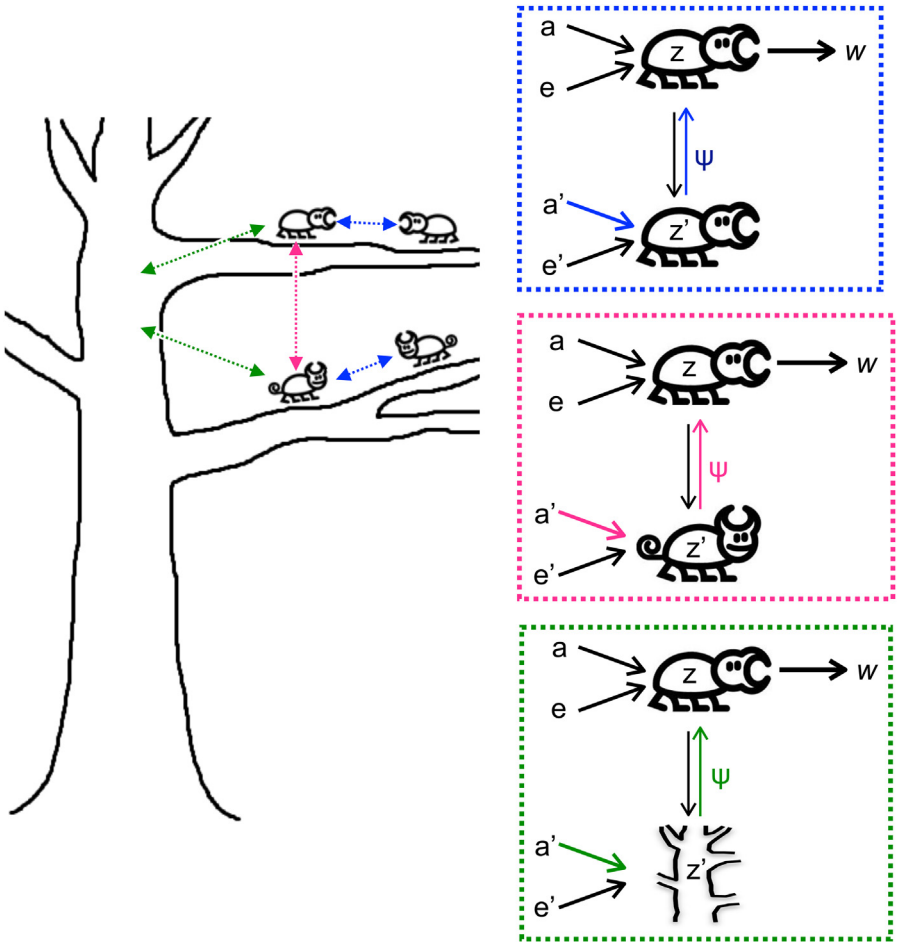

Fig. 1 Architecture of phenotypes whose expression is influenced by the phenotypes of other individuals. In each box, the cartoon insect on the top is the focal individual for this heuristic analysis. We show scenarios for interactions within species (blue lines and box) as well as between species within trophic levels (pink lines and box) and between trophic levels (green lines and box). The two-headed arrows show that the effects may be reciprocal. In each scenario, the phenotype of each individual receives direct inputs from the individual's genotype (a) and environment (e). The plasticity-inducing environmental input derived from the social partner's phenotype is itself also influenced by the social partner's genotype (a′) and environment (e′). The superscripted primes indicate that the genetic, environmental or phenotypic effect arises from the interacting individual. The pathway connecting the genetic component of this indirect effect to the phenotype of the focal individual (i.e., the $a' \rightarrow z' \rightarrow z$ pathway; color arrows in the boxes) is the IGE, the strength and direction of which is described by the interaction coefficient ψ. Note that these effects may be reciprocal, but the colors only indicate the flow towards the focal individual's phenotype. In each box, the fitness of the focal individual (w) is affected by its own phenotype and, indirectly, by the phenotype of the interacting partner.

techniques available for multivariate considerations of IGEs in animal behavior (Bailey *et al.*, 2018). For simplicity, we focus on univariate examples.

Consequences for the Response to Selection

When a trait is influenced by IGEs in the broad sense, its response to selection might not be straightforwardly predicted by the traditional formulation of direct heritability multiplied by the selection differential (Lynch and Walsh, 1998). Instead, it is necessary to take into account the fact that the genetic architecture includes indirect components. This might seem to entail a minor tweak to the decimals, but in fact it represents counter-intuitive adjustments that can bring about major improvements in predicted selection responses (Ellen *et al.*, 2007), with significant consequences for fundamental and applied animal behavior research programs. In the context of animal husbandry, for example, IGEs have been estimated and then used to design selection regimes that reduce mortality in chickens caused by being pecked to death by cage-mates (Muir, 1996; Ellen *et al.*, 2010).

A first general consequence of IGEs is to either augment or dampen the magnitude of the response to selection on the involved traits. This occurs because the complete formulation for the response to selection includes the traditional component of direct heritability multiplied by the selection differential, plus an additional component comprising the IGE multiplied by the selection

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differential weighed by ψ (Moore *et al.*, 1997). Thus, the response to selection may be of greater magnitude with IGEs than without them: this will occur when the sign of ψ is positive, and will be more extreme for larger values of ψ. For instance, if female preferences become stronger when interacting with showier males, one might reasonably predict that any IGEs involved will tend to speed up the evolutionary elaboration of sexual signals (Bailey and Moore, 2012). Conversely, the response to selection due to IGEs is likely to be hindered if ψ is negative, as increased expression of a trait in one partner would be opposed by decreased expression in the other, potentially "softening" responses to selection. In some instances, responses to selection on IGEs could even oppose that on DGEs, resulting in no evolution. Consequently, the covariance (or lack thereof) between IGEs and DGEs is also an important factor in determining responses to selection. The consequences of these effects may include the preservation of direct genetic variation in traits when responses to selection are dulled (Linksvayer and Wade, 2009; Bailey, 2012).

A related consequence is that phenotypic evolution can be sustained even with zero direct genetic variation in a trait. This is a formalization of the insight that responses to selection can continue without genetic variation (West-Eberhard, 1979, 1983, 2014). Three factors are involved: (i) the response to selection in the focal trait has a component constituted by the IGE multiplied by the selection differential weighed by ψ; (ii) when the interacting phenotype of partners evolves, that alone also produces phenotypic evolution in the focal trait through IGEs; and (iii) when the interacting phenotypes are reciprocal, meaning they induce IGEs in each other, there may arise feedback loops that further magnify the response to selection (Moore *et al.*, 1997; Miller and Moore, 2007). We further note that evolution in the interacting phenotype can also generate novel forms in the focal trait that may promote genetic accommodation (West-Eberhard, 2003, 2005; Suzuki and Nijhout, 2006; Renn and Schumer, 2013). A specific example was proposed in an IGE model of sexual conflict, which predicted that IGEs will spur the rapid sequential evolution of multiple male and female antagonistic and counteracting traits, rather than continuous elaboration and counter-elaboration of the same ones (Moore and Pizzari, 2005). There are thus a number of ways in which IGEs drive consequences for the response to selection, that range from speeding or retarding the rate of evolution or holding the phenotype in stasis in spite of ongoing genetic evolution. These consequences depend on the sign and strength of ψ.

Consequences for the Nature of Selection

Interacting phenotypes not only have a special genetic architecture, they also underpin a special relationship between the causes and targets of selection. This is most evident in competition with conspecifics for mates and other resources under sexual and social selection. As the behavior of other individuals constitutes the key selective environment, interacting phenotypes are simultaneously causes and targets of selection: they constitute a selective environment that itself evolves, and that does so in the same time frame as the targets of the selection that they exert (West-Eberhard, 1979, 1983, 2014; Moore *et al.*, 1997; Wolf *et al.*, 1998; Lyon and Montgomerie, 2012; Prum, 2012, 2017).

This dynamic alone can generate powerful evolutionary feedback loops that result in strong selection, rapid evolution, and extravagant phenotypes. With coevolving interacting phenotypes there is no optimum phenotype, and evolution is on-going. Additionally, the phenotypes involved in social interactions may covary. This covariance may result from the IGEs as discussed above, but also from selectivity about whom individuals interact with, or relatedness between the interacting individuals (Wolf *et al.*, 1999; McGlothlin *et al.*, 2010). This covariance further enhances the speed and magnitude of evolution when interacting phenotypes and social selection are involved (Moore *et al.*, 1997; Wolf *et al.*, 1998; McGlothlin *et al.*, 2010; Bailey and Moore, 2012; Rebar and Rodríguez, 2015).

This argument hinges in part on the high levels of plasticity and adjustability in behavior (Zuk *et al.*, 2014; Bailey *et al.*, 2018). However, most other kinds of trait are likely to be correlated in some form to behaviors or other trait types that exhibit social plasticity; e.g., consider a morphological weapon such as an antler and how much of its relationship to fitness hinges on how it is deployed during fights (Moore *et al.*, 1997; McGlothlin *et al.*, 2010). IGEs have been shown to influence non-behavioral traits such as body and genitalia size, development rate, feather condition, anxiety, wound-healing, and immune function (Wolf, 2003; Danielson-François *et al.*, 2009; Biscarini *et al.*, 2010; Ellen *et al.*, 2016; Baud *et al.*, 2017; Marie-Orleach *et al.*, 2017).

An interesting corollary arises from the relationship between trait values and fitness being a function of the interacting partners' phenotypes. In such cases, there arises the possibility of negative-frequency dependence; e.g., as with rock-paper-scissors dynamics (Sinervo and Lively, 1996; Bleay *et al.*, 2007). The resulting cyclical selection may sustain both direct genetic variation in the interacting phenotypes under selection and on-going selection, although there may be no directional phenotypic change (Moore and Pizzari, 2005; Wolf *et al.*, 2008).

Measuring IGEs

There are two basic ways to measure IGEs (Wolf *et al.*, 1998). The first approach involves trait-based estimates. Here, the focus is on how the particular phenotypes of interacting partners influence the phenotype of focal individuals, and this is the framework with which the interaction coefficient ψ is associated. By holding constant the genotype of focal individuals and varying the genotype of the interacting partners, it is possible to regress the focal phenotypes on the phenotypes of the interacting partners. The partial regression coefficient associated with those phenotypes provides an estimate of the magnitude and direction of IGEs

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(Moore *et al.*, 1997; Bleakley *et al.*, 2010). As an example, consider an experiment with inbred lines (such that the genotypes of individuals within each line are effectively identical). Interacting partners and focal individuals could be placed together to measure their behavior (e.g., anti-predator responses), and varying the lines would allow estimating the direction and magnitude of ψ by regressing variation in the behavior of individuals in the focal line on the lines of the interacting partners (Bleakley and Brodie, 2009). Empirical estimates of ψ have often focused on non-behavioral phenotypes such as cuticular hydrocarbons in *Drosophila serrata* (Petfield *et al.*, 2005). Behavioral studies are beginning to provide more, and more detailed, empirical estimates of ψ for a range of traits, and examples in the last decade include antipredator behavior in the guppy *Poecilia reticulata* (Bleakley and Brodie, 2009), female choosiness in the field cricket *Teleogryllus oceanicus* (Bailey and Zuk, 2012), and sociability in *Drosophila melanogaster* (Anderson *et al.*, 2017). As quantitative evidence for IGEs on different behaviors and in different systems accumulates, this can benefit the field of animal behavior at large by facilitating comparative work to test the role of plasticity to the social environment in modulating the evolution of complex animal behaviors (Bailey *et al.*, 2018).

The second way is a "black box" approach that generates a measure, termed performance, which is the variation in a focal phenotype that corresponds to the IGE inputs provided by the other party (Wolf *et al.*, 1998). In other words, performance measures genetic variation in ψ but without measuring the specific traits that make those inputs. As an example, consider an experiment in which a sample of full-sibling families is reared together with a sample of unrelated individuals. Describing variation in the phenotypes of the randomly related individuals according to the components of variation provided by the full-sib families measures performance, corresponding to the IGE inputs arising from those full-sib families (Rebar and Rodríguez, 2013). A key advantage of this approach is that it can be used for IGEs at any level. Imagine an experiment in which a sample of clone lines of a host plant are used to rear randomly related individual insects. Describing variation in the phenotypes of those unrelated individuals according to the components of variation provided by the clone lines also measures performance, corresponding to the cross-trophic IIGE inputs arising from the host plants (Rebar and Rodríguez, 2014a,b, 2015).

The Evolution of ψ: Fine-Tuning the Induction of Plastic Responses in Others

This article may seem to explore IGEs as an abstract theoretical concept with intriguing evolutionary consequences for commonly-studied animal behaviors. But there is an alternative view that brings the concept into sharper focus. IGEs are direct genetic variation in ψ, and ψ arises from individuals' ability to induce plastic responses in others. As such, ψ is a trait. But can it evolve? Darwin (1859) identified the logic for trait evolution: if there is variation in the trait, if that variation is heritable, and if that variation influences survival or reproduction, then the trait necessarily evolves. As the above discussion makes clear, ψ varies, and has measurable direct genetic variation. Geographic variation in ψ has also been documented (Bailey and Zuk, 2012), as well as its capacity to respond to selection (Chenoweth *et al.*, 2010), and its evolutionary dynamics have been theoretically modelled (Kazancioğlu *et al.*, 2012). And it is logical to predict that the induction of plasticity in surrounding individuals is very likely to be related to variation in the fitness of the individual producing those effects. Consequently, we draw attention to the notion that there may be selection on the induction of specific forms of plasticity in other individuals – and, further, that there may be co-adaptation between the induction of plasticity and the plastic response (Moore *et al.*, 1997; Agrawal *et al.*, 2001; Kölliker *et al.*, 2005).

Conclusion

Interacting phenotypes include behavior and many other trait types that exhibit similar dynamics: they constitute the target of selection but also an environmental cause of variation and of selection that can itself evolve. Considering indirect genetic effects – genes in the environment – changes our view of the architecture of trait expression and of the relationship between variation in traits and fitness, bringing insight into processes that have driven evolution of life on Earth.

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See also: **Evolution:** Indirect genetic effects. **Methodology:** Dominance Relationships, Dominance Hierarchies and Rankings.

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