have the potential to evolve (Chenoweth et al. 2010). Consequently, a key issue in understanding the importance of IGEs to phenotypic evolution is determining how long a given social environment will remain stable and how this interacts with DGEs on the phenotype. We think that long-term selection experiments could be useful for such tests. It may be, however, that the very features that ensure behavior is influenced by IGEs are also likely to reduce the long-term impact of IGEs. IGEs may therefore be far more important for short-term evolution.

IGEs can alter both the direction and rate of phenotypic evolution (Wolf et al. 1998). Over the last 10 years, evolutionary geneticists have become increasingly aware of multivariate genetic constraints that arise because selection targets multiple traits that are genetically correlated, meaning there is more genetic variance available for selection in some directions than in others (Blows and Walsh 2009). This not only slows the rate of phenotypic evolution but also critically, biases its direction (Schluter 1996). Do similar multivariate genetic constraints exist for IGEs or do IGEs generate genetic (co) variation in new regions of phenotypic space? If IGEs enhance the evolution of behavior, we expect the latter. One potentially useful way to test for a link between IGEs and behavioral evolution is to estimate vectors of multitrait divergence between populations and assess their orientation with the structure of both the direct and indirect genetic variance-covariance matrix ($\mathbf{G}_{\mathbf{Direct}}$ and $\mathbf{G}_{\mathbf{Indirect}}$). If IGEs reshape evolutionary trajectories, we should be able to detect this by extending these existing multivariate approaches.

In conclusion, we share Bailey et al.'s (2017) view that a deeper understanding of behavior's place in phenotypic evolution requires greater consideration of IGEs. It is worth noting, that studying even DGEs for behavior requires large sample sizes and considerable effort and these requirements are even greater when including IGEs. It is therefore likely that experimental laboratory systems will pave the way for greater synthesis between behavioral ecology and IGE theory.

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If everything is special, is anything special? A response to comments on Bailey et al.

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We propose that indirect genetic effects (IGEs) represent an appealing way to dissect the genetics and evolutionary dynamics of complex phenotypes studied in behavioral ecology. IGEs are complementary to inclusive fitness approaches, but as Kruuk and Wilson (2018) observe, are distinct because they do not require assumptions about relatedness (see also McGlothlin et al. 2014 and McDonald et al. 2017). Thus, IGEs open up the opportunity to study any social interaction and any trait expressed in a social interaction (See Roff 2018). These features of IGEs have enabled behavioral ecologists to study behavior from a slightly different perspective, as an evolutionary feedback process that links individuals and their environments through genes.

The idea of genes in the environment is not new, but the strength and increasing uptake of IGE approaches across the field may derive from the intuitive appeal of evolving environments combined with a robust quantitative method for measuring the effects of social (or other) interactions on key parameters. Behavioral ecology students might certainly find other means to arrive at the conclusions we mentioned in Table 1 (Bailey et al. 2018). We welcome a diversity of approaches. But in the particular studies highlighted, the conclusions make most sense in the light of IGEs, and indeed almost all of them were arrived at using IGE theory. We are reminded of the well-worn adage attributed to statistician George Box (married, of course, to Fisher's daughter so one imagines he appreciated some good theory) that "all models are wrong but some are useful." "Wrong" here means that there are aspects of the model where simplification will fail. So, though Roff (2018) is correct—the model is wrong—IGE models nevertheless have great power to generate testable predictions and novel insights.

Collectively, the responses to our review provide an articulate, helpful guide that anyone studying IGEs would be well advised to consider before planning empirical work. We urge readers to embrace these suggestions, as the field will derive most benefit from well-powered experimental designs and studies that provide innovative advances.

(I) ***Realize your potential.*** Both Kruuk and Wilson (2018) and Chenoweth and Hunt (2018) emphasize that using an IGE framework to test the evolutionary role of behavior in general, or the roles of specific interacting phenotypes such as parental care, dominance, or social learning, requires moving beyond collecting data on evolutionary potential to testing realized evolutionary change. We think the idea of using long-term selection or artificial evolution experiments where possible is laudable, and note Jarrett and Kilner's (2018) engagement with this approach.

(II) ***Seize power.*** As with all work in quantitative genetics, achieving adequate power for robust inference can be logistically daunting. Kruuk and Wilson (2018) highlight the necessity of large-scale studies, and we expect that power would be a particularly acute challenge for empirically testing Roff's (2018) ideas about the impact of nonstatic G matrices, and Chenoweth and Hunt's (2018) approach for comparing $G_{INDIRECT}$ with G_{DIRECT}. We would advise researchers testing the relative influence of IGEs on behavioral versus other traits to start with manageable experiments: a simple comparison of behavioral and nonbehavioral

IGEs would itself require nontrivial effort. The insights afforded by this could then guide whether it would be interesting to extend to a more granular assay of IGEs that includes varying contributions of behavioral interacting phenotypes or group sizes.

(III) ***Be social—or not?*** Garcia-Gonzalez (2018) poses a more existential question about what is social, and we certainly agree that IGEs can arise through interactions that do not involve direct social contact. It is important not to neglect such cases. Roff (2018) also highlights an intriguing, but probably not uncommon, scenario in which only one interacting phenotype is behavioral. IGEs are not unimportant to nonbehavioral traits, as Moore et al. (1997) pointed out in their original paper applying IGEs to social interactions.

We are agnostic (some of us more than others) when it comes to behavior's potentially "special" evolutionary role. If everything is special (Garcia-Gonzalez 2018), then ultimately nothing can be special, so whether behavior possesses qualities which cause it to evolve differently from other phenotypes represents a persistent, unresolved itch in the fields of behavioral and evolutionary biology. We are at pains not to advocate a "prima facie" conclusion to this large, unsolved question, but we do strongly argue for testing it. It is exciting that the theoretical framework of interacting phenotypes and associated quantitative genetic models of IGEs could contribute definitive answers to this debate.

Behavioral ecology is a constantly evolving field that has successfully integrated genetics and optimality to provide insight on the origins and maintenance of fascinating, nonintuitive behaviors. IGEs represent a new feature of behavioral ecology's evolution. Whether they become fixed, go extinct, or bubble along as a balanced or frequency-dependent polymorphism with other genetic frameworks such as inclusive fitness theory or niche construction, will depend on their utility to individual researchers and the insights they deliver. We are eager to see how they fare this ultimate test.

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