

- 1 If Everything is Special, is Anything Special? A
- 2 response to comments on Bailey et al.

**Nathan W. Bailey,<sup>a</sup> Lucas Marie-Orleach,<sup>a</sup> Allen J. Moore<sup>b</sup>**

<sup>a</sup>School of Biology, University of St Andrews, St Andrews, Fife KY16 9TH, UK

<sup>b</sup>Department of Genetics, Department of Entomology, University of Georgia, Athens, GA 30602 USA

Address correspondence to: N.W. Bailey. E-mail: [nwb3@st-andrews.ac.uk](mailto:nwb3@st-andrews.ac.uk).

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

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

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

26  
27 **(I) Realize your potential.** Both Kruuk and Wilson (2018) and Chenoweth and Hunt (2018) emphasise  
28 that using an IGE framework to test the evolutionary role of behaviour in general, or the roles of specific  
29 interacting phenotypes such as parental care, dominance, or social learning, requires moving beyond  
30 collecting data on evolutionary potential to testing realized evolutionary change. We think the idea of  
31 using long-term selection or artificial evolution experiments where possible is laudable, and note Jarrett  
32 and Kilner's (2018) engagement with this approach.

33  
34 **(II) Seize power.** As with all work in quantitative genetics, achieving adequate power for robust  
35 inference can be logistically daunting. Kruuk and Wilson (2018) highlight the necessity of large-scale  
36 studies, and we expect that power would be a particularly acute challenge for empirically testing Roff's

37 (2018) ideas about the impact of non-static G matrices, and Chenoweth and Hunt's (2018) approach for  
38 comparing  $G_{\text{INDIRECT}}$  with  $G_{\text{DIRECT}}$ . We would advise researchers testing the relative influence of IGEs on  
39 behavioural versus other traits to start with manageable experiments: a simple comparison of behavioural  
40 and non-behavioural IGEs would itself require non-trivial effort. The insights afforded by this could then  
41 guide whether it would be interesting to extend to a more granular assay of IGEs that includes varying  
42 contributions of behavioural interacting phenotypes or group sizes.

43

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

50

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

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

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