

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

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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_{INDIRECT} with G_{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

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

64

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