The challenge of estimating indirect genetic effects on behaviour: a comment on Bailey et al.

Invited commentary: Behavioral Ecology

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The notion that behavioural traits 'must often take the lead in evolution' *because* they are 'especially plastic' (West-Eberhard, 2003) sits somewhat uncomfortably with standard quantitative genetic theory. Under simple models, plasticity actually slows evolution: more plastic traits have greater variance, reduced heritability and so lowered expected selection response. Here, Bailey *et al*. (2017) highlight the tantalising possibility that indirect genetic effects (IGEs) could reconcile these contrasting positions. They provide a neat structured list of questions to guide empirical efforts, effectively asking:

1. Is there plasticity in your behavioural trait of interest?

2. Is there plasticity in response to the 'social environment'?

3. Is 'social-environment plasticity' due to IGEs?

4. Do IGEs explain more phenotypic variance for behavioural traits than for other trait types?

We fully agree that assessing the importance, or otherwise, of IGEs for behavioural traits will be valuable and very interesting. However, for anyone contemplating this challenge several points warrant mention. While questions 1 and 2 may be relatively straightforward to address, 3 and 4 require complex analyses, starting with the decision about whether to use trait-based or variance-partitioning approaches (see Boxes 1 and 2, Bailey et al. 2017). This decision must be made partly on pragmatic grounds, and we expect variance partitioning to be more tractable in many cases: most importantly, it avoids the need to have correctly measured all partner traits

with causal effects (see Bijma, 2014 for comprehensive discussion). It can also be applied to Q2 (as well as Q3), as social plasticity implies "indirect phenotypic effects" that can be estimated prior to the more data-demanding task of partitioning IGEs. Our comments here therefore relate to this variance-partitioning approach.

Several key issues need to be borne in mind for IGE variance-partitioning. Firstly, dyadic interactions – such as those between mothers and offspring, mating partners or contest antagonists – are relatively straightforward to model, but other scenarios are not. Interactions can involve multiple partners, groups of differing size (e.g., number of competing nestlings), and ambiguity in defining group membership. The model presented (Equation 2.1) assumes a uniform group size and fixed group membership with no inter-group interactions. This will suit many experimental studies, but some thought is needed for application to less controlled scenarios (Wilson, 2014).

Second, statistical models will probably need to be more complex than suggested in Box 2. Repeated observations are increasingly common (and welcome) in behavioural studies, but require explicit modelling of non-genetic among-individual differences to avoid overestimation of genetic variance (Bijma et al., 2007; Kruuk and Hadfield, 2007). This consideration applies equally to indirect effects. While 'group' effects may be sufficient when group membership is fixed (Bijma et al., 2007), in

other situations indirect 'permanent environment' effects are required to avoid inflation of IGE variance (e.g. Wilson et al., 2011).

Third, Q1-4 are not fully sufficient to characterise the impact of IGEs on evolutionary potential. IGEs represent an additional source of genetic variance, but one that can constrain as well as facilitate selection responses. Evolutionary potential is defined by the 'total' variance in breeding values, which depends on the variances of direct and indirect genetic effects, but also, critically, on their covariance (see Equation 2.2). The latter can – and sometimes must – be negative, such that IGEs *reduce* evolvability. They may even reduce the 'total heritable variation' to nothing; in fact IGE models can provide useful fodder for efforts to explain phenotypic stasis in the face of directional selection (Wilson, 2014). Answering 'yes' to all the questions posed above means IGE are important for determining the evolutionary potential of behaviour, but not necessarily that they increase it.

In conclusion, we welcome the suggestion that behavioural ecology should better incorporate IGEs. Our thinking about social evolution has long been dominated by relatedness, but IGEs represent a second, distinct mechanism by which associations can arise between the genes of an actor and the fitness of a recipient (Bijma and Wade, 2008). Empirical dissection of IGEs is therefore exciting new territory, but it is also challenging, and requires both careful construction of appropriate models and *extremely* powerful data-sets. Arguments that behaviour is 'special' are not entirely

convincing to us – though perhaps because we are not true behavioural ecologists –
but such studies will certainly be valuable, regardless of whether they support the
idea that IGEs increase evolvabilities of behavioural traits or not. We also think there
is great potential in studies that: firstly, explore the consequences of IGEs on
multivariate phenotypes (including, for instance, morphology and life history as
well as behaviour); and, secondly, recognize that social plasticity may involve both
IGEs and GxE simultaneously, and hence the possibility of (direct) G x (indirect) G
interactions. Finally, we hope that growing interest in IGEs will help correct the
current imbalance in the literature, where theoretical and methodological treatments
abound but empirical estimates, especially from natural systems, are still scarce.

References

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