

Indirect Genetic Effects in Behavioural Ecology: Does Behaviour Play a Special Role in Evolution?

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Lay Summary: Behaviour is highly flexible, but does this make it special compared to other types of traits? We review how considering indirect genetic effects—the influence of genes expressed by social partners—can inform behavioural ecology research by improving predictions of behavioural optima in different social, evolutionary and ecological contexts. We argue that this framework is ideal for empirically testing behaviour’s proposed, yet heavily debated, unique role in shaping evolutionary patterns and processes.

1 **ABSTRACT**

2 Behaviour is rapidly flexible and highly context-dependent, which poses obvious challenges
3 to researchers attempting to dissect its causes. However, over a century of unresolved debate
4 has also focused on whether the very flexibility and context-dependence of behaviour lends it
5 a unique role in the evolutionary origins and patterns of diversity in the Animal Kingdom.
6 Here we propose that both challenges can benefit from studying how indirect genetic effects
7 (IGEs: the effects of genes expressed in one individual on traits in another individual) shape
8 behavioural phenotypes. We provide a sketch of the theoretical framework that grounds IGEs
9 in behavioural ecology research and focus on recent advances made from studies of IGEs in
10 areas of behavioural ecology such as sexual selection, sexual conflict, social dominance, and
11 parent-offspring interactions. There is mounting evidence that IGEs have important
12 influences on behavioural phenotypes associated with these processes, such as sexual signals
13 and preferences and behaviours which function to manipulate interacting partners. IGEs can
14 also influence both responses to selection and selection itself, and considering IGEs refines
15 evolutionary predictions and provides new perspectives on the origins of seemingly
16 perplexing behavioural traits. A key unresolved question, but one that has dominated the
17 behavioural sciences for over a century, is whether behaviour is more likely than other types
18 of traits to contribute to evolutionary change and diversification. We advocate taking
19 advantage of an IGE approach to outline falsifiable hypotheses and a general methodology to
20 rigorously test this frequently proposed, yet still contentious, special role of behaviour in
21 evolution.

22 *“Thus, behavior being especially plastic, behavior must often take the lead in*
23 *evolution.”* Mary Jane West-Eberhard (2003), p. 180

24

25 **INTRODUCTION**

26 **Is behaviour special?**

27 Those who study animal behaviour are often motivated by the observation that behaviours
28 can appear to be counterintuitive, making it necessary to dissect and reveal their costs and
29 benefits, plus the trade-offs inherent in long-lived organisms. This has often been approached
30 using an optimality framework, which defines evolutionarily stable outcomes under such
31 conditions (Parker and Maynard Smith 1990). Classic examples of counter-intuitive
32 behaviours that have been studied using optimality include sexual cannibalism, conspicuous
33 sexual signalling, altruism, and aggression. However, this framework has a potential
34 limitation. Optimality treats such behaviours as an emergent property of many underlying,
35 potentially unknown or even unknowable, mechanistic influences on different constituent
36 traits – an approach that Alan Grafen (1984) described as a phenotypic gambit, where the
37 necessary mechanisms including genetics are assumed to allow unconstrained evolution to an
38 optimum. Ignored causal influences range from molecular signalling pathways, to
39 morphological structures, to nervous connections, to environmental context. Thus, the
40 phenotypic gambit has significant limitations (Moore and Boake 1994; Golmulkiewicz 1998;
41 Hadfield et al. 2007; Rubin 2016), not the least of which is ignoring evolutionary dynamics
42 on the way to an equilibrium (regardless of whether it is reached). It is perhaps ironic that
43 behaviour appears to be one of the least suited types of traits to study using this framework
44 (Roff 1996; Fawcett et al. 2013). This may be due in part to the high degree of reversibility
45 and context-dependence of many behaviours, particularly those expressed in the context of

46 social interactions.

47 It may be that the simultaneous integration of many different causal factors is what
48 makes behaviour such a challenging phenotype to study mechanistically: behaviour can be
49 highly reversible, variable, inconsistent, contextual and ephemeral. Yet, the complexity of
50 inputs to behaviour may also contribute to its alleged special nature. For well over a century,
51 its flexibility and environmental sensitivity have been invoked to support a special role in
52 evolution, for example by biasing the direction of evolutionary responses (Baldwin 1902),
53 exposing new variation to the action of selection (Wcislo 1989), acting as a pacemaker that
54 regulates the rate of diversification (Mayr 1963), disproportionately leading genetic evolution
55 (West-Eberhard 2003, Zuk et al. 2014, Robinson and Barron 2017) or inhibiting evolution
56 (Huey et al. 2003, Price et al. 2003). Unusual roles for plasticity and behaviour have also
57 been invoked to argue for reformulating the fundamental structure of evolutionary theory as
58 we know it, an assertion that has provoked scepticism and contentious debate (Laland et al.
59 2014). Arguments for behaviour's special role in evolution often invoke mechanisms such as
60 genetic assimilation, accommodation, or shifting plasticity thresholds to link non-genetic
61 behavioural variation to longer-term genetic evolution. Such processes have theoretical
62 backing (e.g., Lande 2009, Chevin and Lande 2015), and some empirical support (e.g.
63 Waddington 1953, Badyaev 2009, Sikkink et al. 2014). Verbal arguments have suggested that
64 the link between behaviour and evolution is expected to be strongest in circumstances where
65 behaviour is sensitive to variation in the social environment (e.g., Bateson 2004), and social
66 effects have been proposed to play a correspondingly greater role in behavioural evolution in
67 species with highly complex social interactions, such as the eusocial Hymenoptera
68 (Linksvayer 2015).

69 In this article, we describe how behavioural ecologists are increasingly adopting a
70 research approach that considers genes expressed in social partners—indirect genetic effects,

71 or IGEs—to be a part of the environmental context that shapes animal behaviour. We explore
72 how IGE frameworks provide behavioural ecologists with tools to improve optimality
73 predictions and obtain more focused solutions to research challenges, for example by better
74 understanding the causes of behavioural variation within and between species. We suggest
75 that empirically examining the role of IGEs in shaping behaviour will provide important
76 insights for the field of behavioural ecology. Beyond this, however, we suggest a
77 methodological approach using IGEs to rigorously test whether behaviour does, or does not,
78 play a unique role in evolution.

79

80 **BEHAVIOUR AND IGEs**

81 **The reversibility, context-dependence, and sensitivity of behaviour**

82 Competing definitions of behaviour abound, but one commonly accepted defining
83 characteristic is that behaviour entails a response to environmental stimulus (Levitis et al.
84 2009). Thus, flexibility or plasticity is an inherent property. This flexibility has led to the
85 well-known debate over nature and nurture, where simple causes (genes) are rightly viewed
86 as insufficient explanations for the expression of a behavioural phenotype. Of course, this
87 reflects a false dichotomy (both nature and nurture must contribute for any trait to exist) but it
88 also reflects a sense that there is inherent complexity in behaviour that may not exist in other
89 phenotypes. Incorporating IGEs allows nature to be nurture as well, resolving some of these
90 concerns (Moore et al. 1997, McGlothlin et al. 2010). Social interactions induce IGEs, which
91 partly explains why the flexible properties of behaviour make it prone to unexpected
92 evolutionary dynamics or phenotypic equilibria that can appear non-adaptive. The apparent
93 susceptibility of behavioural phenotypes to social influences could make them especially
94 prone to IGEs, providing a testable, though presently hypothetical, evolutionary genetic
95 explanation for their proposed role in evolution.

96

97 What are, and are not, IGEs?

98 A framework for studying behaviour was specifically developed to incorporate genetics and
99 further refine the evolutionary understanding of traits identified as fundamental in
100 behavioural ecology – the Interacting Phenotype approach (Moore et al. 1997, 1998). This
101 approach incorporates IGEs, and it recognizes that many of the attributes that make
102 understanding behavioural evolution difficult arise from behaviour expressed in social
103 interactions. This characteristic is part of what generalises and extends IGE models from
104 maternal effects, which are a specific case of IGEs (Wolf et al. 1998, McAdam et al. 2014).

105 IGEs result in altered evolutionary trajectories (Moore et al. 1997, McGlothlin et al.
106 2010). Examples where social environments and IGEs are predicted to affect trait expression
107 and evolution involve interacting phenotypes such as communication, signalling, aggression,
108 dominance, learning, sexual conflict and sexual selection (Moore et al. 1998, Bleakley et al.
109 2010, Wolf and Moore 2010). But despite the intended connection to behavioural ecology,
110 research on IGEs has until recently been concentrated in the fields of quantitative and
111 behavioural genetics. From such studies, we know that variation in the social environment
112 animals experience can generate evolutionary feedbacks mediated by IGEs if the social
113 environment consists of genetically varying individuals; such feedbacks arise because the
114 environment itself can evolve (Moore et al. 1997, Bailey 2012). The strength and direction of
115 IGEs can also evolve over time and across populations (Chenoweth et al. 2010, Bailey and
116 Zuk 2012, Kazancıoğlu et al. 2012, Edenbrow et al. 2017), and associated social selection is
117 predicted to vary accordingly (McGlothlin et al. 2010). In recent years, IGEs have been
118 incorporated into animal and plant breeding studies to more accurately predict evolutionary
119 responses in agriculturally valuable traits, such as growth rate, thermal tolerance, and
120 infection risk (Camerlink et al. 2013, 2014, 2015; Costa e Silva et al. 2013; Anche et al.

121 2014; Muñoz et al. 2014; Alemu et al. 2016; Baud et al. 2017). A substantial literature
122 explores the mathematical approaches used to study IGEs. For general overviews see
123 Bleakley et al. (2010), Wolf and Moore (2010), and McAdam et al. (2014); for a treatment of
124 quantitative modelling and parameter estimation issues, see Bijma (2010, 2014).

125 IGEs do not require a conceptually new entity. These are additive genetic effects in
126 individuals that contribute to a social environment that affects the trait of another (focal)
127 individual, and which can itself evolve. As noted by Mary Jane West-Eberhard (1979 p. 228)
128 when discussing social evolution and extravagant characters, "... a change improving
129 competitive ability is always favored... Each successive improvement sets a new standard
130 which the next can profitably surpass. This is due to the fact that conspecific rivals are an
131 environmental contingency that can itself evolve. In that respect social evolution is
132 comparable to the coevolution of predator-prey, parasite-host interactions...". Thus
133 evolutionary biologists have long recognized social environments as providing novel
134 evolutionary dynamics. Because of IGEs, contributions to social traits can covary genetically,
135 even when the genes act in different individuals. It is this covariance that results in unusual
136 evolutionary dynamics. When an individual expresses a behaviour, that phenotype
137 reflects the inherent properties of the individual (e.g. physiological state, genes, experiences,
138 and learning) as well as external abiotic and biotic influences. However, when the
139 environment is social, then genetic differences amongst these interacting individuals
140 contribute to differences in the social environment, creating a heritable environmental effect .
141 In other words, genes and the environment are confounded. Heritable social effects create
142 non-linear evolutionary dynamics when incorporated into evolutionary models (Moore et al.
143 1997, McGlothlin et al. 2010). When specific phenotypes are being studied, the interaction
144 coefficient, ψ (ψ), describes the importance of the interaction for the phenotype that is
145 expressed. For traits unaffected by social interactions, $\psi = 0$. In traits where the social

146 interaction reduces trait expression, $\psi < 0$, but where traits are increased in expression
147 because of the social interaction, $\psi > 0$. Box 1 illustrates the concept and highlights recent
148 studies that have estimated ψ or its multivariate counterpart, Ψ .

149

150 The importance of timing and sequence in social interactions

151 The timescale over which individual phenotypes change because of IGEs influences the
152 outcome of evolutionary dynamics, depending on the number and frequency of social
153 interactions (McGlothlin et al. 2010, Saltz 2013, Schneider et al. 2016; Anderson et al. 2017,
154 Edenbrow et al. 2017). In addition, the phenotypic equilibrium for a trait affected by IGEs is
155 determined partly by the whether the IGE is reciprocal or not (i.e. the same trait influences its
156 own expression in focal and partner individuals, as in aggressive escalations, versus a focal
157 trait that is affected by a different trait in an interacting partner, as in maternal care). When
158 IGEs are particularly strong and reciprocal, theoretical arguments have predicted that the trait
159 equilibria of phenotypes involved become unstable, possibly leading to increasingly extreme
160 phenotypic fluctuations, oscillations, or even the disintegration of social groups (Trubenová
161 et al. 2015).

162 The influence of timing of social interactions has been considered most extensively in
163 the context of agonistic encounters and animal contests. For example, aggressive conflicts
164 between groups of green woodhoopoes (*Phoeniculus purpureus*) that occur in the morning
165 generate long-term effects that increase social bonding behaviours within groups later in the
166 evening, such as allopreening and roosting (Radford and Fawcett 2014). Experience of same-
167 sex contests in juvenile female burying beetles (*Nicrophorus vespilloides*) increases
168 reproductive output later in life, possibly as a result of increased post-hatching brood care,
169 regardless of the outcome of the contest (Pilakouta et al. 2016). Learning from social
170 experience is a related, and widespread, example of how the phenotypic impact of the social

171 environment can be temporally separated from individual encounters. Learned mate
172 preferences are now commonly studied (Dukas 2005, Verzijden et al. 2012), and when such
173 changes in female mating behaviour involve IGEs, their impact on sexual selection and
174 diversification can be significant (Bailey and Moore 2012).

175 Time-delays between when a social interaction occurs and a focal individual's
176 phenotype changes will affect the phenotypic trait values that are ultimately available to the
177 action of selection. Time-courses of IGEs can be linked to underlying physiological and
178 neuronal processes that shape trait expression, and vary widely. IGEs can influence “slow-
179 changing state variables”, such as metabolism-dependent body growth, in addition to “fast-
180 changing state variables”, such as near-instantaneous behavioural adjustment during an
181 agonistic encounter (Niimalä and Santostefano 2015). Examples of both are readily found in
182 the literature. For example, IGEs on growth in pigs arising from behavioural phenotypes such
183 as aggressive biting are not only documented, but have been successfully selected in artificial
184 breeding programs (Camerlink et al. 2013, 2014). In contrast, isogenic focal *Drosophila*
185 *melanogaster* males vary in how much they physically tap interacting partners of different
186 genotypes with their prothoracic legs during bouts of interaction lasting only minutes, a
187 behaviour that might reflect gustatory sampling or aggression (Bailey and Hoskins 2014).
188 Not only the timing of socially plastic responses underlying IGEs, but when during life any
189 fitness effects of those changes are manifested, will ultimately impact evolutionary dynamics
190 shaping behaviour (Schneider et al. 2016). If the phenotypic effects of IGEs are invisible to
191 selection, they will not contribute to evolutionary dynamics.

192

193 **IGEs IN BEHAVIOURAL ECOLOGY RESEARCH**

194 Improving optimality predictions using IGEs

195 Adopting an interacting phenotype approach would be merely a curiosity if it provided no

196 insights over approaches based on the phenotypic gambit. Optimality has provided a useful
197 framework for making predictions in experimental animal behaviour research programmes.
198 Understanding causes of variation is a cornerstone of behavioural ecology, taught in
199 undergraduate courses and featured in canonical texts (Davies et al. 2012). Yet optimality
200 assumes a population has reached an evolutionarily stable state. This represents a limitation
201 for behaviour that has been suggested to reflect ignorance of mechanisms such as genetics
202 (Moore and Boake 1994). Animal behaviours can often appear counter-intuitive or non-
203 adaptive at first blush (Bailey 2013), and the extent to which dissecting the underlying causal
204 mechanisms of behaviour can enlighten us about its ultimate causes represents a persistent
205 tension within the field (Tinbergen 1963, Mayr 1961, Laland et al. 2011). The theoretical
206 framework of IGEs provides one way of reconciling optimality predictions and variable
207 behaviour. In the remaining sections, we describe how IGEs have been detected in
208 behavioural studies to date, what insights have been gained, and why behavioural ecology
209 studies can benefit from including IGEs in the toolkit of “proximate causes” of behavioural
210 variation. We finish by proposing that behavioural ecologists can use IGEs as a powerful
211 conceptual tool to inform, with quantitative predictions and data, the debate about whether
212 behaviour is a unique sort of trait with emergent properties making it difficult to characterise
213 genetically, but at the same time lending it a special role in evolution.

214

215 Theoretical insight into the influence of IGEs on behaviour

216 The role of the social environment in shaping behaviour has been a dominant theme in
217 behavioural ecology studies, and there is a growing interest in incorporating mechanisms into
218 such studies (Hoffman et al. 2014), including IGEs . The question is whether considering a
219 given behaviour as susceptible to genes expressed in social partners lends insight to our
220 understanding of the forces that cause that behaviour. Drown and Wade (2014) pitted

221 genotypes with varying degrees of sensitivity to the social environment against one another in
222 a series of quantitative genetic models, to assess the contribution of heritable variation in the
223 environment on evolutionary rates. They found that heritable components of the environment,
224 IGEs, can generate runaway evolution when they become linked with genetic variants that
225 control responses to that social environment. Rapid coevolutionary dynamics are a specific
226 consequence of responses to genes in the social environment, rather than responses to abiotic
227 environments.

228 Rapid evolution can become runaway. Bailey and Moore (2012) examined the
229 evolution of sexual signals and mating preferences and found that a key determinant of
230 whether IGEs accelerate or retard sexual trait elaboration is the sign and magnitude of the
231 interaction coefficient ψ , which alters the influence of trait-preference genetic covariance
232 during runaway co-evolution. Accumulation of genetic covariances between sexual traits and
233 preferences are a fundamental property of Fisher's original model of sexual selection (Fisher
234 1915, 1958), but incorporating IGEs counterintuitively suggested that trait-preference
235 covariances can be smaller than expected while still allowing runaway to occur. This finding
236 may help to reconcile a pervasive lack of evidence for expected trait/preference genetic
237 covariances in empirical studies (Greenfield et al. 2014). IGEs have also been modelled in
238 sexual conflict scenarios, and when strong, they are predicted to stimulate rapid evolutionary
239 proliferation of adaptations and counter-adaptations above standard predicted rates (Moore
240 and Pizzari 2005).

241 Evolutionary dynamics that can arise through IGEs address two issues affecting
242 commonly studied traits in behavioural ecology such as ornaments, mate preferences and
243 armaments. The first is that IGEs might provide an evolutionary genetic mechanism for the
244 prediction that such traits are labile in varying social environments, which has been
245 confirmed in numerous phenotypic studies on learning and mating behaviour (Dukas 2005;

246 Kozak and Boughman 2008, 2009; Bailey et al. 2010; Bailey 2011; Rebar et al. 2011, 2016;
247 Auld et al. 2016; Rebar and Rodríguez 2016). Thus, IGEs allow the flexibility we see in
248 social behaviour to be consistent with standard evolutionary theory. The second is that they
249 refine our expectations of what is an optimal behaviour in circumstances where IGEs are
250 expected, enabling a better explanation of seemingly perplexing traits. Empirical research is
251 now beginning to put these ideas to the test.

252

253 Empirical evidence for IGEs in behavioural ecology research

254 Explicitly considering IGEs in behavioural studies provides a more accurate understanding of
255 what causes behavioural variation, and in some cases can fundamentally change our
256 interpretation of those causes. IGEs for sexual traits such as signals and female mating
257 preferences have now been documented in several invertebrate systems, and in a smaller
258 number of studies, have been demonstrated to evolve. In *Drosophila melanogaster*, IGEs
259 exerted through social interactions alter the composition of sexually selected male cuticular
260 hydrocarbons (CHCs) (Kent et al. 2008). In the related species *D. serrata*, the genotype of
261 interacting females has been found to explain nearly a fifth of the variance in male CHC
262 profiles (Petfield et al. 2005), and the expression of two methyl-branched alkanes important
263 for sexual signalling in males can be artificially evolved under different female social
264 environments (Chenoweth et al. 2010). In one strain of the lesser waxmoth *Achroia grisella*,
265 male body mass and the pulse-pair rate and peak amplitude of ultrasonic advertisement songs
266 were found to be affected by IGEs (Danielson-François et al. 2009). In different populations
267 of the field cricket *Teleogryllus oceanicus*, female choosiness in mating trials is affected
268 differently by the previous experience of singing males or silence, suggesting population-
269 level variation in the interaction coefficient ψ for these traits (Bailey and Zuk 2012).

270 Researchers have also quantified IGEs on traits that mediate sexual conflict (e.g.

271 Signor et al. 2017). In the hermaphroditic flatworm *Macrostomum lignano*, there is striking
272 heterogeneity in the presence, strength and direction of IGEs on multiple morphological and
273 behavioural traits with expected roles in sexual conflict, such as gonad size and copulation
274 latencies (Marie-Orleach et al. 2017). *Macrostomum lignano* performs an intriguing
275 behaviour after copulation in which individuals apply their pharynx on top of their own
276 sperm storage organ and appear to suck it (Schärer et al. 2004, Vizoso et al. 2010). This
277 behaviour is facultative and thought to be involved in removing from storage some
278 components of the recently received ejaculate. Optimality models not considering IGEs
279 would predict that sperm recipients suck only when it is beneficial to them, e.g. when they do
280 not need extra sperm for fertilisation. However, the propensity to suck depends to some
281 extent on the genetics of the sperm donor, which opens the possibility for manipulation of the
282 partner's suck behaviour through prostate gland secretions (Marie-Orleach et al. 2013, Marie-
283 Orleach et al. 2017). Thus, this behaviour would appear counterintuitive, or non-optimal, if
284 IGEs are not considered. Other examples exist in the field of animal breeding, in which
285 programs considering IGEs have been shown to improve the response of selection for various
286 traits of interest to breeders (e.g., growth rates in pigs, or plumage condition in laying hens)
287 (Camerlink et al. 2013, 2015, Brinker et al, 2014). In Table 1, we provide additional
288 examples illustrating how considering IGEs can modify our interpretations of a behaviour's
289 causes, and reveal unsuspected evolutionary forces influencing their expression.

290 In laboratory mice, a cross-fostering experiment demonstrated that offspring genotype
291 influences maternal care behaviours, providing a genetic mechanism mediating the evolution
292 of parent-offspring conflict (Ashbrook et al. 2015). As these were lab mice, the researchers
293 mapped genomic loci that might play a role in mediating those effects, providing clues about
294 causal offspring behaviours, such as solicitation, to which mothers responded. In *D.*
295 *melanogaster*, the genotype of male mating partners exerts a significant impact on copulation

296 duration, illustrating that it is not solely under female control (Edward et al. 2014).
297 Nevertheless, other female traits that would be expected to be susceptible to sexual conflict
298 dynamics such as egg production showed no IGEs (Edward et al. 2014). Another *D.*
299 *melanogaster* study recovered a significant effect of male partner identity on female
300 fecundity, consistent with a male IGE affecting female fitness components (Tennant et al.
301 2014). Male IGEs affecting female fecundity appear to be exerted through male mitonuclear
302 epistasis in seed beetles (*Callosobruchus maculatus*), suggesting a complex interplay
303 between organelle-specific IGEs and sexual conflict (Immonen et al. 2016).

304 Non-sexual social behaviours are also impacted by IGEs. Normally the purview of
305 inclusive fitness theory and kin selection, behaviours critical to the functioning of animal
306 societies are increasingly being studied from the viewpoint of interacting phenotypes and
307 IGEs (Linksvayer 2006, Linksvayer 2015, Linksvayer and Wade 2016). In *Pogonomyrmex*
308 *californicus*, a harvester ant, variation in the social composition of founding groups of queens
309 in cooperative colonies determines behavioural outcomes in aggression and brood care
310 phenotypes (Clark and Fewell 2013). IGEs have been documented across a range of
311 additional social traits, including paternal care (Head et al. 2012), social dominance (Moore
312 et al. 2002, Wilson et al. 2011), agonistic encounters (Wilson et al. 2009; Santostefano et al.
313 2016), group antipredator behaviour (Bleakley et al. 2009, Edenbrow et al. 2017), and
314 breeding date in birds (Germain et al. 2016). In the mosquitofish *Gambusia holbrooki*, direct
315 genetic effects (DGEs) influence the number of social partners that males of different colour
316 morphs encounter, illustrating how DGEs and IGEs can covary (Kraft et al. 2016), a critical
317 parameter influencing evolutionary dynamics (Bijma 2014).

318 IGEs are also relevant to the expression of behaviours within interspecific and multi-
319 trophic interactions. Interspecific IGEs can have a wider impact on the evolution of
320 community assemblages and ecosystem functioning (Genung et al. 2013a, b). For example,

321 the genotype of a parasitoid wasp *Aphidius ervi* influences whether infected aphids
322 (*Acyrtosiphon pisum*) remain on or abandon their host plant, and dictate the final location of
323 death of aphids who choose to remain (Khudr et al. 2013). Male treehoppers (*Enchenopa*
324 *binotata*) use substrate-borne vibratory communication as a sexual signal, and the genotypes
325 of plants used as vibratory substrates affects both the expression of male signals and female
326 mating decisions (Rebar and Rodríguez 2014a, b). Genotypic variation among substrate
327 plants also mediates the phenotypic covariance of the treehoppers' sexual trait and preference
328 (Rebar and Rodríguez 2015).

329

330 **TESTING BEHAVIOUR'S "SPECIAL ROLE" IN EVOLUTION**

331 Behavioural susceptibility to IGEs

332 Until now, we have documented how IGEs can affect the expression of commonly studied
333 behaviours, helping to explain unexplained variation. It is also important to consider how
334 behavioural ecology studies can inform the broader evolutionary implications of IGEs. Are
335 behaviours especially prone to responding to IGEs in a way that accelerates, decelerates or
336 otherwise modifies evolutionary trajectories? Over the past several decades, the field of
337 behavioural ecology has shown how exquisitely sensitive animal behaviour is to the social
338 environment, even in species that typically spend their lives in asocial states. In addition,
339 there is increasing evidence that IGEs affect many behaviours, and thus processes, that
340 behavioural ecologists study. But is behaviour unique in this respect? Some would argue yes:
341 part of the call for an extended evolutionary synthesis relies on the intuition that the extreme
342 responsiveness of behaviour to the environment and unexpectedly rapid evolutionary change
343 requires a new evolutionary explanation (Laland et al. 2011, 2014, 2015). However, IGEs and
344 interacting phenotype theory provide an explanation for extreme plasticity and variability, for
345 evolutionary change without DGEs, and for rapid evolution of traits that are sensitive to

346 social environments, that is fully consistent with standard evolutionary theory.

347

348 What proportion of V_P is $V_{E(\text{social})}$?

349 The starting point for predicting which traits in focal individuals are most likely to contribute

350 to evolutionary dynamics through IGEs—and testing whether behavioural traits are

351 systematically over-represented in this category—is to establish whether any of the traits in

352 question respond to variation in the social environment. If so, then this is an interacting

353 phenotype. The insight that behaviour can be affected by social interactions may be obvious,

354 but traits such as morphology also respond to variable social environments, often through

355 density-dependent or maternal effects. Secondly, we can ask whether genetic heterogeneity

356 among individuals affects the contributions of the social environment to phenotypes. If so,

357 then IGEs exist. The relative importance of IGEs can be measured against the contributions

358 of DGEs. Studies that have quantified IGEs using either variance partitioning or trait-based

359 approaches on multiple phenotypes have tended to find heterogeneity across assayed traits in

360 their responsiveness to genes in the social environment. For example, ca. 18% of heritable

361 variation in growth rate in the flour beetle *Tribolium castaneum* was influenced by IGEs,

362 while no such influence was documented for other life-history traits in the same study (Ellen

363 et al. 2015). A trait-based analysis of five antipredator and social behaviours in the guppy

364 *Poecilia reticulata* found evidence for reciprocal IGEs on all traits, but only a limited number

365 of non-reciprocal IGEs, and their directions and magnitudes varied (Bleakley et al. 2009). In

366 the latter study, the extent of schooling behaviour in focal individuals was negatively related

367 to the tendency of social partners to remain near a model, whereas the amount of time a focal

368 individual spent in proximity was positively related to agitation behaviour in interacting

369 partners.

370 The final requirement for testing whether the flexibility of behaviour makes it

371 particularly susceptible to IGEs is to systematically compare different types of traits. The
372 variance-partitioning approach (Box 2) can quantify the amount of phenotypic variance
373 associated with different sources using standard quantitative genetic approaches.
374 Environmental influences on a given trait's expression can be subdivided into effects of the
375 physical environment and those of the social environment (Moore et al. 1997; Bijma 2014).
376 Standardizing trait values is necessary if traits are measured in units, but there are no
377 restrictions on the types of traits that can be measured. The key question is whether the
378 partitioning differs for behavioural traits versus other traits such as morphology, life history,
379 or physiological attributes.

380 Nested hypotheses can be used to interrogate this question: can we first reject the null
381 hypothesis that there are no environmental influences on trait expression (i.e. plasticity – this
382 requires testing in multiple environments)? Next, can we reject the null hypothesis that there
383 are no effects of the social environment on trait expression (i.e., interacting phenotypes – this
384 requires testing over variable social environments)? If an interacting phenotype exists, can we
385 reject the null hypothesis that there are no IGEs arising from that social environment effect
386 (IGEs– this requires pedigrees or breeding designs to identify genetic effects)? In the final
387 analysis, a proportion of explained variance can be assigned at each level of this hierarchical
388 model. The process can be iterated for a panel of different traits, marrying the ability of the
389 trait-based interacting phenotype approach to interrogate specific phenotypes with the ability
390 of the variance partitioning approach to estimate relative contributions of any IGEs. An
391 important consideration is to avoid biasing the outcome when selecting such a panel of traits;
392 for example, by focusing on behaviours known to be particularly labile.

393 Partitioning variance for a panel of randomly-chosen traits can seem a daunting task,
394 but a recent study examining the effects of IGEs on health and disease factors in lab mice,
395 *Mus musculus*, is one of the first tests using such an approach and provides a guide forward.

396 Baud et al. (2017) assayed over 100 phenotypes related to health and disease after housing
397 mice of different genotypes together. In their first experiment using two inbred lines of mice,
398 the authors detected IGEs in 11 out of 50 phenotypes assayed. In a separate experiment with
399 an outbred population, the authors detected IGEs in 43 out of 117 traits assayed, and in 8 of
400 those 43, IGEs explained a greater proportion of variance than DGEs (Baud et al. 2017). The
401 design of the experiment did not enable a conclusion regarding the likelihood of behavioural
402 traits experiencing IGEs versus other sorts of traits, owing to the non-random selection of
403 assayed phenotypes .

404 IGEs in more than one phenotype allow estimates of the multivariate matrix of
405 interaction coefficients, Ψ (e.g. Bleakley and Brodie III 2009, Marie-Orleach et al. 2017),
406 and identification of candidate interacting phenotypes underlying ‘hidden’ IGEs by
407 comparing values of ψ across multiple traits (Bailey and Hoskins 2014). It might be similarly
408 possible to test hypotheses about the role of behaviour in evolution in a more trait-aware
409 fashion, using comparisons of ψ . However, the field still lacks a systematic comparison of
410 amounts of variance explained across different categories of traits. Such studies could use
411 panels of inbred lines (e.g. Fuller and Hahn 1996, Bailey and Hoskins 2014, Baud et al.
412 2017), or pedigreed populations (e.g. Wilson et al. 2009, Germain et al. 2016). Experimental
413 evolution approaches would also allow an assessment of how IGEs versus DGEs contribute
414 to selection responses, which could be used to test the evolutionary potential of different
415 types of traits. Work that explicitly tests whether behavioural traits are more often subjected
416 to IGEs would inform debate in behavioural ecology over the role of behaviour as a
417 phenotypic ‘arena’ in which sexual selection, conflict, and dominance are enacted in animals,
418 and ultimately address the question of whether IGEs exerted through behaviour are
419 particularly important—or not—in leading evolutionary change.

420

421 **SUMMARY AND RECOMMENDATIONS**

422 Accounting for the influence of genes on the social environment can improve optimality
423 predictions that might be otherwise thwarted by the complex, flexible, multivariate nature of
424 most behaviours (Table 1). Just as Hamilton's Rule provided a gene-centric impetus for better
425 optimality predictions about altruism, kin selection, animal societies, group selection, etc., we
426 suggest that considering IGEs in the social environments of animals, broadening social to
427 include any interaction, will facilitate a better understanding of the costs and benefits of
428 behaviour that appears unusual, improbable, or inexplicable. Behavioural ecologists are just
429 beginning to use the framework of IGEs to test how genes expressed in interacting social
430 partners affect expression of behaviours in a variety of contexts, but models suggest that
431 IGEs should matter in sexual selection, sexual conflict, the maintenance of dominance
432 hierarchies, and evolution of sociality. IGEs can lead to quantifiably more rapid responses to
433 selection. As we have reviewed, these efforts resolve mismatches between predicted and
434 observed genetic architectures of secondary sexual traits and mating preferences, informing
435 the paradox of the lek, and providing quantitative tests about the number and nature of
436 sexually antagonistic adaptations and counter-adaptations. The nascent empirical literature on
437 IGEs in behavioural ecology indicates that formulating hypotheses and predictions that
438 incorporate genetic effects in interacting social partners can similarly enhance the abilities of
439 behavioural ecologists to test causes of behavioural variation.

440 The field of behavioural ecology has an opportunity to capitalize on a well-developed
441 quantitative genetic framework to inform a longstanding debate about the unusual role of
442 behaviour in evolution. Are behavioural traits more susceptible to IGEs compared with
443 morphology, life history, and physiology? Depending on the answer to that question,
444 systematically examining whether different types of interacting behavioural phenotypes are
445 more influenced by IGEs than others will further clarify how and when behaviour might

446 cause unique evolutionary effects. Susceptibility to IGEs may drive distinctive evolutionary
447 dynamics in behaviours involved in, for example, conflict, cooperation, or reproductive
448 interactions. We consider it to be an intriguing possibility that behaviour might play a unique
449 role in ‘leading evolution’, but despite over a century of intense interest, this debate is
450 unresolved. IGEs provide behavioural ecologists with a means for putting this idea to the test
451 with falsifiable hypotheses, quantitative predictions, and hard data.

452

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457

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743 **Box 1. The interaction coefficient, ψ : a standardized estimator of IGEs when traits are**
744 **known *a priori*.**

745

746 Trait-based approaches for estimating IGEs focus on how previously identified traits interact,
747 and therefore require more emphasis on *a priori* hypotheses. Focal and interacting behaviours
748 are frequently known in advance in behavioural ecology studies, which may account for the
749 increasing popularity of estimating ψ . Other resources provide detailed mathematical
750 treatment of ψ and guidance on how to estimate it (e.g. Bleakley et al. 2010, Schneider et al.
751 2016), so we confine our remarks to a brief conceptual overview highlighting the importance
752 of the parameter (and its multivariate counterpart, Ψ) plus several recent studies that have
753 estimated it.

754 A significant advantage of estimating ψ , as opposed to utilising the variance-
755 partitioning approach of quantifying IGEs outlined in Box 2, is that it does not necessarily
756 require detailed genetic information. The parameter was originally derived as an analogue of
757 the maternal effect coefficient, m , and can be estimated by regressing standardized
758 phenotypic values of focal genotypes on the trait values of their interacting partners (Moore
759 et al. 1997). If trait values are mean centred with unit variance prior to entry into such a
760 model, then ψ_{ij} is the partial regression coefficient describing how trait i in focal individuals
761 covaries with trait j in interacting partners. The resulting estimates of ψ range from [-1,1] and
762 indicate both the magnitude and direction of IGEs. Reciprocal trait interactions occur when
763 the same trait is examined in both individuals, and the matrix Ψ reflects all pairwise and
764 reciprocal trait interactions when more than one trait is measured. Thus, IGEs can be
765 quantified conveniently in studies where it is possible to manipulate genotypes using different
766 strains or inbred lines. Even when strains or lines are not readily available, as often occurs in
767 behavioural ecology studies, other means for partitioning genetic variation in interacting

768 partners can be used, for example by taking advantage of naturally-occurring alternative
769 phenotypes with a genetic basis (e.g. Bailey and Zuk 2012). An equation adapted from two
770 recent studies (Marie-Orleach 2017, Signor et al. 2017), derived originally from Moore et al.
771 (1997), is illustrative:

772

773

774 Eqn. 1.1

$$z_i = \alpha_i + \gamma_i l + \sum_{j=1}^n \psi_{ij} z'_j + \sum_{j=1}^n \gamma_{ij} (l \times z'_j) + \varepsilon_i$$

775

776

777 This model describes how the expression of a trait in a focal individual, z_i , is affected by
778 IGEs caused by interaction with social partners, z'_j . For every trait j in the interacting partner,
779 the magnitude and direction of IGEs on trait i in the focal individual can be estimated by ψ_{ij} .

780 Studies of behaviour can often take advantage of distinct genetic strains or inbred lines, and

781 one way to measure line-specific values of ψ is to run separate models for each line (e.g.

782 Signor et al. 2017). In the example above, however, estimates of ψ_{ij} are modelled

783 simultaneously for different focal lines by examining the interaction between a main effect of

784 focal line, l , and z'_j for each interacting trait. Errors and intercepts are given by ε_i and α_i ,

785 respectively. More complex models can be built upon this framework, for example

786 multivariate formulations in which relationships between multiple focal and interacting traits

787 $z_{i_{1...m}}$ and $z'_{j_{1...m}}$ can be captured by an $m \times m$ matrix (a square matrix when the same suite of

788 traits is measured in both focal and interacting individuals; the diagonal entries representing

789 reciprocal trait interactions):

790

791

792

793 Eqn. 1.2

$$\mathbf{\Psi} = \begin{bmatrix} \psi_{1,1} & \cdots & \psi_{1,m} \\ \vdots & \ddots & \vdots \\ \psi_{m,1} & \cdots & \psi_{m,m} \end{bmatrix}$$

794

795

796 Critically, ψ (and in the multivariate case, $\mathbf{\Psi}$) are key determining factors of the unique
797 dynamics caused by IGEs. For example, the interaction coefficient plays a critical role in
798 determining the consequences of IGEs in models of sexual conflict (Moore and Pizzari 2005),
799 Fisherian sexual selection (Bailey and Moore 2012), and the evolution of IGEs themselves
800 (Kazancıoğlu et al. 2012).

801 Genetically distinct strains of study animals have been used in a variety of systems to
802 estimate ψ . Such studies vary in the level at which genetic differences between interacting
803 partners are manipulated. At one extreme, population-level differences in ψ for a component
804 of female mate choice in the field cricket *Teleogryllus oceanicus* rests on the assumption of
805 population genetic structure, and therefore provides inference about differences in IGEs at the
806 population level (Bailey and Zuk 2012). In contrast, several studies provide strain-specific
807 estimates of ψ , for example for predator avoidance behaviours in the guppy *Poecilia*
808 *reticulata* (Bleakley et al. 2009), sexually antagonistic mating behaviours in the
809 hermaphroditic flatworm *Macrostomum lignano* (Marie-Orleach et al. 2017), and locomotion
810 in the fruit fly *Drosophila melanogaster* (Signor et al. 2017). The latter three studies used a
811 small number of inbred lines and report that ψ not only varies for different behavioural traits,
812 but also that different lines show different values of ψ . Earlier work also used experimental
813 evolution in lines of *D. serrata* to demonstrate evolution of ψ for sexually-selected cuticular
814 hydrocarbon profiles (Chenoweth et al. 2010). In *D. melanogaster*, a multiple regression
815 approach was used with 50 interacting, inbred lines from the Drosophila Genetic Resource
816 Panel to identify candidate interacting traits affecting focal male tapping behaviour, which

817 was demonstrated to be affected by IGEs but required interrogation to identify traits involved
818 with the IGE (Bailey and Hoskins 2014). While there is clearly heterogeneity in the approach
819 for manipulating the genotype of interacting individuals in such studies, the use of a common,
820 standardized estimator allows comparison of the relative importance of IGEs across different
821 species, traits and contexts.

822 **Box 2. Behaviour's special role in evolution: are behavioural traits especially susceptible**
823 **to IGEs?**

824

825 Flexibility is a defining feature of behaviour. While multifactorial causes, reversibility and
826 context-dependence can make behavioural traits less repeatable, posing technical challenges
827 to their accurate quantification, the same characteristics have also been argued to confer
828 special properties to behaviours that other traits do not share. For example, unusually high
829 plasticity can be advantageous in situations where quick or reversible phenotypic responses
830 are required, such as sexual selection, sexual conflict, signalling, or dominance interactions
831 (Mayr 1964, 1974, West-Eberhard 1989, 2003). However, there is unresolved debate around
832 the ultimate consequences of this sort of phenotypic lability. A simplified version of the
833 question underpinning this debate is whether phenotypic flexibility of behaviour (i.e. a
834 tendency to high plasticity) causes it to have a special role in processes such as those
835 mentioned above, and in evolutionary change more generally. If behaviour is thus set apart
836 from morphological, life history or physiological traits, studies seeking to explain the causes
837 or consequences of variation in animals will benefit from a better understanding of
838 phenotypic expectations for behavioural traits. This can be informed by quantifying and
839 comparing the influence of IGEs. Here we outline a method to do so.

840 It would be profitable to test the prediction that IGEs are more common and of greater
841 magnitude for behavioural traits, compared with other types of traits. If supported, this would
842 provide evidence that IGEs represent at least one distinct, quantifiable mechanism underlying
843 a unique role for behaviour in determining patterns of organismal diversity more generally.
844 This is analogous to the approach adopted by Mousseau and Roff (1987) comparing
845 heritabilities of life-history traits, morphological traits, behavioural traits and physiological
846 traits. The idea is to partition sources of phenotypic variation into direct and indirect genetic

847 influences, the former arising from individual actors and the latter from genes expressed by
848 other individuals with whom they socially interact.

849 There are two ways to do this (McGlothlin and Brodie 2009). If the specific traits and
850 their influences are known, a trait-based approach is the most powerful as it allows a
851 consideration of the extent that the social environment matters for each trait (estimated using
852 the interaction coefficient ψ , cf. Moore et al. 1997; see Box 1). However, researchers often do
853 not know ahead of time the traits that should be measured or that are having an influence; we
854 often know that the social environment matters, but no more than that (Bailey and Hoskins
855 2014). Under such conditions a variance-partitioning approach is informative. Extensive
856 mathematical treatments of IGEs have been published elsewhere, and interested readers are
857 encouraged to consult these resources to learn more about the practicalities of experimental
858 and breeding designs (e.g. Moore et al. 1997; Bijma 2010, 2014; Bleakley et al. 2009;
859 McGlothlin and Brodie 2009). Here, we focus on parameters of key interest that are
860 accessible to researchers for quantifying the existence, prevalence, magnitude, and potential
861 consequences of IGEs.

862 Considering a finite population of conspecifics, a variance-partitioning can be
863 described with mathematical expressions. Following the derivations in Bijma (2014), we can
864 describe how the total phenotypic variance, σ_p^2 , is composed of variance from DGEs caused
865 by genes expressed within individuals that affect their own phenotypic trait values, σ_{aD}^2
866 (subscripts a denoting additive genetic effects and D for direct effects), variance arising from
867 genes expressed in interacting social partners (IGEs), σ_{aS}^2 (subscript S showing that the
868 genetic variance arises from social interactions) scaled by the number of non-focal interacting
869 partners ($n - 1$), plus all other sources of non-heritable variation, ϵ_i :

870

871 Eqn. 2.1

$$\sigma_p^2 = \sigma_{aD}^2 + (n - 1)\sigma_{aS}^2 + \epsilon_i$$

872 Throughout this explanation, variance terms representing DGEs are coloured in blue, while
873 those representing IGEs are coloured red. For our purposes, we are only interested in genetic
874 sources of phenotypic variation, whether arising directly within focal individuals ($\sigma_{a_D}^2$), or
875 from genes expressed in interacting social partners ($\sigma_{a_S}^2$). The importance of direct and
876 indirect genetic effects can be assessed by examining their contribution to the *evolutionary*
877 *potential* of a population of individuals. This is equivalent to the total variance in the
878 breeding value (cf. Bijma 2014), which is comprised of additive effects a_D and a_S :

879

880

881 Eqn. 2.2

$$\text{evolutionary potential} \sim \sigma_{a_D}^2 + 2(n-1)\sigma_{a_{(D,S)}} + (n-1)^2\sigma_{a_S}^2$$

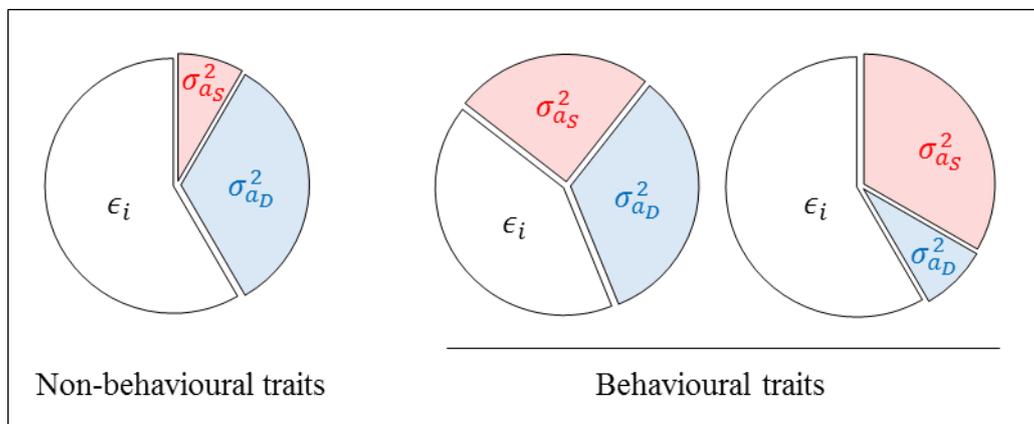
882

883 Evolutionary potential describes the possible response to selection. If selection is
884 assumed to be constant, the expression above illustrates how IGEs can affect the ultimate
885 evolutionary outcome of traits. The middle term in purple represents covariance between
886 direct and indirect genetic effects. Its importance is beginning to be investigated in empirical
887 behavioural studies, and on a functional level this can be thought of as the degree to which
888 the trait that responds to social environments in a focal individual also reflects the social
889 environment that the focal individual provides to others – strong, positively associated effects
890 will tend to enhance evolutionary potential, while opposing effects will impede the response
891 to selection.

892 If IGEs affect behaviour disproportionately, then this leads to the prediction that
893 IGEs should be detected more frequently for behavioural traits than non-behavioural traits,
894 provided traits are surveyed in an unbiased manner and measured on a standardized scale. In
895 addition, the approach described above can be used to quantify magnitudes of components
896 and compare them among trait types. To make this comparison, we advocate calculating

897 evolvability, which is the coefficient of variation standardized by the mean. This approach
 898 allows comparison of the relative importance of IGEs and DGEs under standard quantitative
 899 genetic assumptions, and is similar to that used by Baud et al. (2017) in controlled
 900 experiments with laboratory mice. A caveat is that transforming phenotypic values prior to
 901 calculating genetic variances, as was done using a Box-Cox power transformation to satisfy
 902 model assumption in Baud et al. (2017), can complicate subsequent comparison of
 903 evolvabilities (Garcia-Gonzalez et al. 2012). Thus, to enable inference about both the *relative*
 904 influence of IGEs, and to compare differences in *absolute* evolutionary potential contributed
 905 by IGEs across traits or organisms, we advocate comparing mean-standardized variances
 906 (Hansen et al. 2011, Garcia-Gonzalez et al. 2012). The figure below shows a comparison of
 907 hypothetical variance components for different traits, in which we have arbitrarily set the
 908 total phenotypic variances to be equal for purposes of illustration.

909



910

911

912 Consider a moderately heritable trait, where approximately 30% of the total variance reflects
 913 the contributions (or variance associated with) additive genetic effects. If it is non-
 914 behavioural, the prediction is that any variance component describing IGEs will be relatively
 915 small (left). If behavioural traits are more susceptible to IGEs, indirect genetic variance may
 916 represent a greater proportion of the overall environmental variance (middle), in which case

917 non-heritable effects ϵ_i are diminished. However, IGEs may also represent a relatively larger
918 fraction of genetic variance overall even if non-heritable effects remain constant (right).
919 Comparing the relative proportions of phenotypic variance explained by DGEs versus IGEs
920 among different traits addresses the question: “are IGEs more important than DGEs for
921 behaviour, but not other traits?”, but absolute, mean-standardized variances can also be
922 compared to ask “what is the absolute importance of IGEs to the evolvability of different trait
923 types, regardless of DGEs?”

924 A finding that behaviour is more affected by IGEs would support its hypothesized
925 distinctive role in evolution, and lend insight into its expression in circumstances that interest
926 behavioural ecologists. However, failure to establish a difference between behavioural and
927 non-behavioural traits would be interesting as well. Such an outcome would not negate the
928 proposition that behaviour can be involved in unique evolutionary dynamics as a result of its
929 lability, for it may be that such dynamics involve only a specific, restricted set of behaviours.
930 However, failing to generally distinguish behavioural traits versus other types of traits based
931 on an important genetic cause, IGEs, would stimulate more general reflection on the
932 distinctive biological properties of *behaviour* as a unitary phenomenon, and perhaps return us
933 to ideas developed during the origins of modern ethology, animal behaviour and behavioural
934 ecology, encapsulated by Lorenz’s (1941) famous observation in a comparative study of birds
935 that “[t]he few morphological characters distributed in the table are intended to show how
936 similar their distribution is in many cases to that of the *innate behaviour patterns*”.

Table 1: Examples of behavioural traits for which considering IGEs has changed inference about the causes of variation, including maternal care, social behaviours, sexual selection, and animal breeding examples from recent studies.

Trait description	Interpretations when IGEs are omitted	Interpretations when IGEs are considered
Maternal care in laboratory mice (<i>Mus musculus</i>).	Maternal care is only determined by the mother's own genes, and her (non-genetic) environmental conditions. Mothers invest optimally in maternal care to optimise their inclusive fitness.	The offspring genetics also influences maternal care, which enables optimal co-adaptation between the levels of maternal care and offspring solicitation (Ashbrook et al. 2015).
Maternal care in the European earwig, <i>Forficula auricularia</i> .	Maternal care is only determined by the mother's own genes, and her (non-genetic) environmental conditions. Mothers invest optimally in maternal care to optimise their inclusive fitness.	Investment in maternal care is also influenced by the genetics of the offspring and the father. This implies that maternal care is governed by mutualistic and antagonistic coevolution between the mother, the father, and their offspring (Meunier and Kölliker 2012).
Antipredator behaviour in guppies, <i>Poecilia reticulata</i> .	Antipredator behaviour expressed only at the benefits of the individual expressing it. The evolution of social behaviour and cooperation among unrelated social partners is paradoxical.	The genetics of social partners influence antipredator behaviour, which facilitate the evolution of antipredator behaviour, cooperation, and social behaviour (Bleakley and Brodie III 2009).
Song produced by the male lesser waxmoth, <i>Achroia grisella</i> , involved in female mate choice	The male song is only determined by the male's own genes, and his (non-genetic) environmental conditions. Female mate choice should rapidly erode the genetic variation in song production (The Lek paradox).	The male song is also modulated by the genetics of male social partners, which contributes to maintain genetic variation in song production (Danielson-François et al. 2009).
The suck behaviour facultatively expressed after copulation by the hermaphroditic flatworm, <i>Macrostomum lignano</i> , during which worms apply their pharynx on top of their own sperm storage organ and appear to suck.	Worms suck when it is beneficial to them, e.g., no need of extra sperm for egg fertilisation, use ejaculate as food resource, cryptic female choice.	The suck behaviour is also the target of manipulation by the mating partners at their own benefits, e.g., use sperm for egg fertilisation (Marie-Orleach et al. 2013, 2017).
Growth rate in domestic pigs, <i>Sus scrofa</i> , used in breeding programs.	Growth rate is only determined by the pig's own genes and its (non-genetic) environmental conditions. Artificial selection on high growth rate should produce pigs that grow faster.	Pig growth rate is also influenced by social interactions with their penmates, such as aggressive and biting behaviours (Camerlink et al. 2015). Breeding programs accounting for IGEs provide better outcomes (Muir 2005).
Male leg tapping in the fruit fly <i>Drosophila melanogaster</i> , in which the prothoracic leg is extended and contacts the cuticle of another individual.	Tapping behaviour is controlled by focal males and is expressed in the context of chemosensory sampling or aggressive interactions.	Expression of tapping behaviour depends on elicitation or opportunity controlled by the genotype of interacting partners. A combined trait-based and variance partitioning approach identified a behavioural trait, the startle response, as a possible mediator of this IGE (Bailey and Hoskins 2014).