

1 Genetic correlations across genetically  
2 determined and developmentally plastic  
3 alternative reproductive tactics  
4

5 Jessica K. Abbott<sup>1,2</sup>, Oscar Rios-Cardenas<sup>3</sup> & Molly Morris<sup>4</sup>  
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7 1. Section for Evolutionary Ecology, Department of Biology, Lund University, 10 Sölvegatan 37, 22362  
8 Lund, Sweden. Email: [Jessica.abbott@biol.lu.se](mailto:Jessica.abbott@biol.lu.se)

9 2. Corresponding author

10 3. Red de Biología Evolutiva, Instituto de Ecología, A. C. Xalapa, Veracruz, Mexico

11 4. Department of Biological Sciences, Ohio University, Athens OH, USA  
12

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## 24 Abstract

25 Alternative reproductive tactics occur when individuals of the same sex have a suite of  
26 morphological and/or behavioural traits that allow them to pursue different reproductive strategies.  
27 A common pattern is e.g. the existence of “courter” and “sneaker” tactics within males. We have  
28 previously argued that alternative reproductive tactics should be subject to genetic conflict over the  
29 phenotypic expression of traits, similar to sexual antagonism. In this process, which we called intra-  
30 locus tactical conflict, genetically determined tactics experience conflicting selection on a shared  
31 phenotypic trait, such as body size, but a positive genetic correlation between tactics in body size  
32 prevents either tactic from reaching its optimum. Recently, other authors have attempted to extend  
33 this idea to developmentally plastic alternative reproductive tactics, with mixed results. However, it  
34 is not clear whether we should expect intra-locus tactical conflict in developmentally plastic tactics  
35 or not. We have therefore run a series of simulation models investigating under what conditions we  
36 should expect to see positive estimates of the inter-tactical genetic correlation, since a positive  
37 genetic correlation is a prerequisite for the existence of intra-locus tactical conflict. We found that  
38 for autosomal, X-linked, and Y-linked genetically-determined tactics, estimated inter-tactical genetic  
39 correlations were generally high. However, for developmentally plastic tactics, the genetic  
40 correlation depends on the properties of the switching threshold between tactics. If it is fixed, then  
41 estimated genetic correlations are positive, but if there is genetic variation in the switch-point, then  
42 any sign and magnitude of estimated genetic correlation is possible, even for highly heritable traits  
43 where the true underlying correlation is perfect. This means that caution should be used when  
44 investigating genetic constraints in plastic phenotypes.

45

## 46 Introduction

47 Alternative reproductive tactics (ARTs) are different ways of achieving reproductive success within a  
48 sex, and often involve suites of behavioral, morphological and life history traits. ARTs are expected  
49 to evolve when sexual selection is strong and multiple strategies are possible (reviewed in Shuster  
50 and Wade 2003). Studies of ARTs across a range of taxa (reviewed in Oliveira et al. 2008) have led to  
51 a better understanding of the maintenance of genetic variation given strong sexual selection, as well  
52 the adaptive nature of that variation (i.e. the best phenotype for using one tactic is often not the  
53 best phenotype for a different tactic). The discontinuous expression of at least one or more traits in  
54 either males or females is often the first indication of an ART (e.g. Gross 1996; Brockmann 2001).  
55 However, there is a growing appreciation for the role of intralocus tactical conflict (IATC) in  
56 constraining the evolution of differences between the ARTs (tactical dimorphism), such that even  
57 traits that are more or less continuous within a sex may have more than one underlying optimum  
58 (Abbott et al. 2019).

59 Individuals from different ARTs will share many homologous traits, however if the optimal state for  
60 these traits differ depending on the ART, this will lead to opposing selection (i.e. tactically disruptive  
61 selection). When traits that are genetically correlated across the ARTs are not at their adaptive  
62 optimum, tactically disruptive selection can generate intralocus tactical conflict (Morris et al. 2013;  
63 Buzatto et al. 2015). Studies of intralocus tactical conflict have the potential to increase our  
64 awareness of cases where expressed states are not necessarily optimal due to the evolutionary  
65 constraints (e.g. slower growth rates, a lack of behavioural plasticity; Abbott et al. 2019). IATC also  
66 has the potential to lead to a better understanding of the role of ecological variation across  
67 populations in producing the patterns of divergence between ARTs, as well as provide us with a  
68 better understanding of the relationship between ARTs and rapid speciation (Abbott et al. 2019).  
69 The criteria for demonstrating intralocus tactical conflict include a positive genetic correlation  
70 between the ARTs, detecting different optima for the trait across ARTs, and evidence that the ARTs  
71 are not at their optima for the trait (Morris et al. 2013).

72 Inter-tactical genetic correlations measure the extent of similarity between the additive effects of  
73 alleles when expressed in different tactics. The ideal method for determining inter-tactical genetic  
74 correlations when ARTs are genetically fixed is a multigeneration half-sib breeding design, followed  
75 by the statistical decomposition of the genetic variance into its many different components  
76 (Falconer and Mackay 1996). Given the prevalence of genetic correlations across the sexes even  
77 when sexual dimorphism has evolved (e.g. Harano et al. 2010; Poissant et al. 2010), it can be  
78 assumed that these correlations are not temporary or transitional stages, highlighting the  
79 importance of their estimation across ARTs as well as across the sexes. By current estimations, most

80 ARTs are developmentally plastic (Oliveira et al. 2008); however, this consensus may change as the  
81 studies of the proximal mechanisms behind these ARTs increase.

82 West-Eberhard (1986) described how the loss of an alternative phenotype could play a role in  
83 speciation through the release “from constraints of having to accommodate multiple alternatives”  
84 (pg 1388) within a shared genome. And yet, the idea that developmental plasticity decouples the  
85 development of the alternative morphs, allowing them to evolve independently, is prevalent in the  
86 literature (reviewed in Tomkins and Hazel 2007). Therefore, a better understanding of the potential  
87 for genetic correlations between ARTs that are both genetically fixed and developmentally plastic is  
88 needed to determine the extent to which intralocus tactical conflict may be influencing the evolution  
89 of ARTs. There are a few empirical studies that have examined genetic correlations across  
90 developmentally plastic ARTs. Considering male traits across two species with tactically dimorphic  
91 male ARTs that are environmentally influenced, Pike et al. (2017), detected very weak genetic  
92 correlations in one species (earwigs, *Forficula auricularia*), and significant correlations in another  
93 species (acarid mites, *Rhizoglyphus echinopus*). The genetic correlations in the acarid mite have been  
94 further confirmed through artificial selection experiments (Buzatto et al. 2018).

95 Genetically-determined ARTs can be divided into two types that could potentially differ in their  
96 propensity for genetic correlations. First, allelic variation at autosomal loci can influence  
97 polymorphisms, as in a marine isopod (Shuster and Wade 1991). Second, genetic polymorphisms  
98 may be correlated with the genes influencing sex, as in the swordtail fishes where male ARTs have  
99 been linked to genetic variation on the Y-chromosome (Zimmerer and Kallman 1989; Lampert et al.  
100 2010). Developmentally plastic ARTs, on the other hand, have been proposed to evolve via  
101 environmental thresholds. In this model, the environment influences alternative phenotypes  
102 through a genetically-determined threshold (Hazel et al. 1990; Hutchings and Myers 1994), which  
103 may be able to respond rapidly to artificial selection (Emlen 1996). Studies of several species have  
104 provided evidence for the environmental threshold model of developmentally plastic ARTs: Atlantic  
105 salmon, where males can either mature sexually early in life in freshwater or more commonly only  
106 after completing a migration at sea (Lepais et al. 2017); horned beetles, where some males develop  
107 horns and some do not (Emlen 1996); and bulb mites (Buzatto et al. 2015). In the current study, we  
108 use simulations to examine the potential for genetic correlations across ARTs that vary in their  
109 underlying mechanisms, including an autosomal ART locus, an X- or Y-linked ART locus, a fixed  
110 threshold for plastically determined tactics, and genetic variation in the switching threshold between  
111 plastic tactics.

112 Intertactical additive genetic correlations, similar to  $r_{mf}$  between the sexes (Lande 1980), are  
113 predictive of the potential for future independent evolution of the ARTs within a population. Here  
114 we considered the genetic correlation of traits across ARTs that are not directly linked to the locus  
115 (or loci) producing the ART. For example, in the case of the autosomal supergene producing  
116 differences across male ARTs in ruffs (Küpper et al. 2015), the inversion has linked a suite of traits  
117 involved in the ARTs. However, by considering the extent to which these correlations will be present  
118 for traits not directly linked to the ARTs, we can determine the extent to which IATC can influence  
119 and potentially constrain their evolution. Our results suggest that for autosomal, X-linked, and Y-  
120 linked genetically-determined tactics, estimated genetic correlations are, as expected, generally  
121 high. However, for developmentally plastic tactics, the estimated genetic correlation depends on the  
122 properties of the switching threshold between tactics, such that genetic variation in the switching  
123 threshold can lead to a range of estimates even when the true underlying genetic correlation is  
124 perfect.

## 125 Simulation model

126 In the case of genetically-determined tactics, all simulations assume a single ART locus with two  
127 alternative alleles producing different alternative reproductive tactics. If tactic is developmentally  
128 plastic, then the phenotype determines the threshold for switching between tactics. Different  
129 relationships between the phenotype and the threshold are considered (see below). The trait that  
130 can experience tactical antagonism is a quantitative trait determined by many loci that are spread  
131 throughout the genome (e.g. body size). This means that there is no effect of linkage between the  
132 ART locus and the trait.

133 The simulations are designed in such a way that they resemble the simplest form of an animal  
134 model:

$$135 \quad y_i = \mu + a_i + e_i$$

136 Where  $y_i$  is the phenotypic trait value of individual  $i$ ,  $\mu$  is the phenotypic mean in the population,  $a_i$   
137 is the breeding value, and  $e_i$  is the residual error. Parameters in the simulations are therefore the  
138 number of families (fixed at 1000), the population mean (arbitrarily fixed at 50), the population  
139 standard deviation (used in randomly generating a breeding value for each family; arbitrarily fixed at  
140 5 unless otherwise stated), the within-family standard deviation (used in generating developmental  
141 noise for each individual, and equal to the residual standard error), the magnitude of the trait  
142 difference between the ARTs (arbitrarily fixed at 5 unless otherwise stated), and the offspring  
143 number (arbitrarily fixed at 10 unless otherwise stated). Heritability measured as  $V_a/V_p$  is therefore  
144 equal to the population SD/(population SD + within-family SD). For developmentally plastic tactics

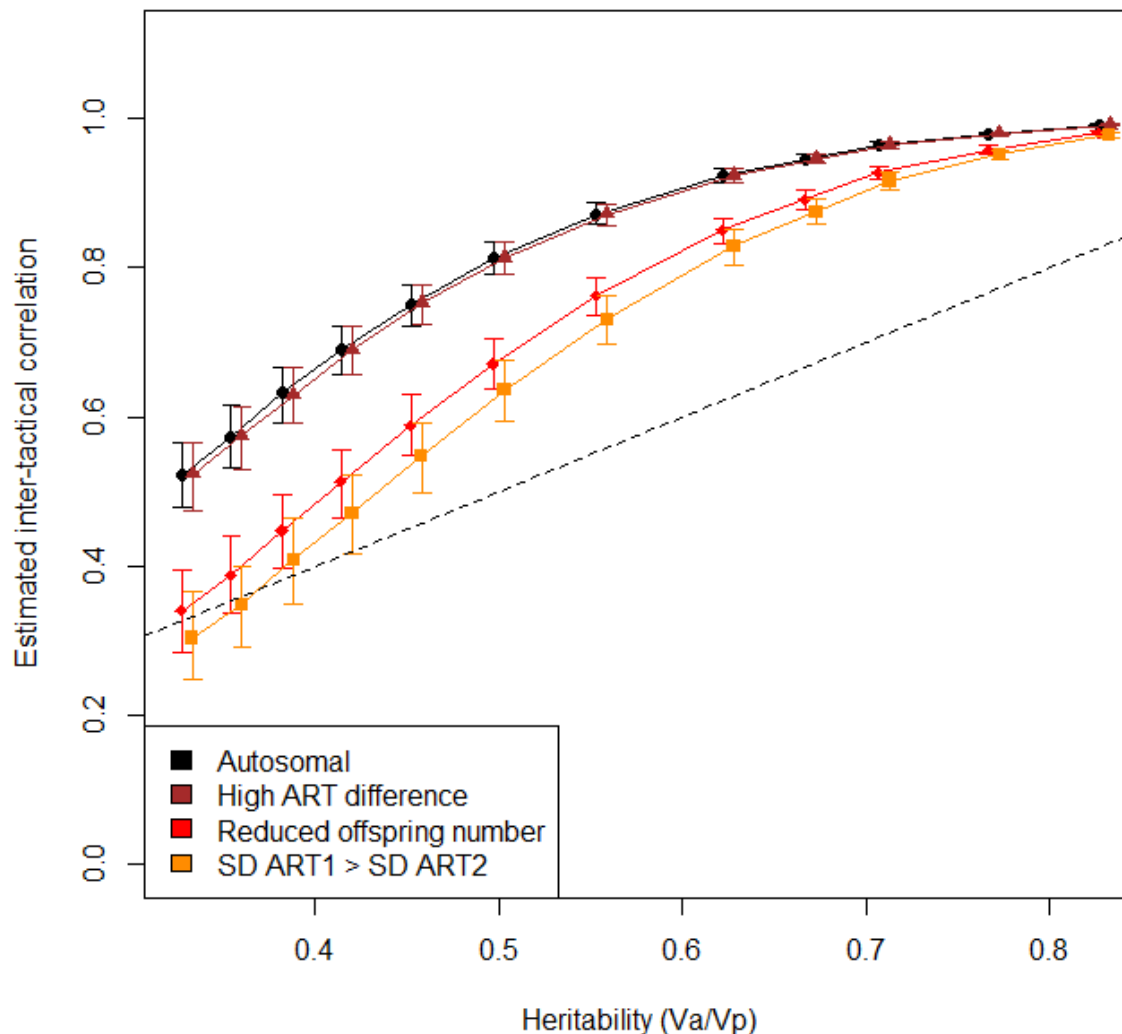
145 there is an additional parameter for the switching threshold. The inter-tactical correlation was  
146 estimated from within-family means, as in Buzatto et al. (2015). For Y-linked tactics, we also included  
147 an analysis using MCMCglmm (see below). Datasets were simulated 1000 times each, in order to  
148 obtain information about stochastic variation in correlation estimates for a given set of parameter  
149 values.

150 We examine several different scenarios, including an autosomal ART locus, an X- or Y-linked ART  
151 locus, a fixed threshold for switching tactics, and various ways of relating the switching threshold to  
152 the breeding value. Note that in all cases the underlying genetic architecture of the quantitative trait  
153 is a perfect genetic correlation between tactics, so what we investigate with our simulations is  
154 variation in the empirical estimate of the genetic correlation, and how well it corresponds to the  
155 true genetic architecture.

## 156 Autosomal ART locus

157 This is the simplest possible case, and was simply analysed to provide a baseline for comparison with  
158 the other scenarios. We assume that at least some families are capable of producing a mix of  
159 different ARTs, for example when two heterozygotes for a dominant ART locus mate with each other  
160 and produce offspring of all possible genotypes. We varied the population standard deviation, the  
161 within-family standard deviation, offspring number, and the mean trait difference between ARTs,  
162 and investigated heritability and the magnitude of the inter-tactical genetic correlation.

163 We found that, as expected, estimated inter-tactical correlations were high for an autosomal ART  
164 locus, and increased with increasing heritability (Figure 1). This is a logical result; if the variation  
165 within a family is as large as (or larger than) the variation in breeding values across the entire  
166 population, it will be more difficult to detect the inter-tactical correlation. Interestingly, we could  
167 also show that the estimate of the inter-tactical genetic correlation was often higher than the  
168 heritability of the trait (Figure 1, dashed line shows 1:1 relationship), which suggests that the  
169 underlying genetic architecture is more important in determining the estimated genetic correlation  
170 than the observed heritability. Increasing or decreasing the trait difference between the tactics does  
171 not affect these conclusions, but assigning different levels of developmental noise to the two ARTs,  
172 or reducing family size, both decrease the estimate of the correlation (Figure 1). This is also an  
173 intuitive result since there will be more error in the estimate when the family size is low. The effects  
174 of trait difference between tactics and family size is consistent across all other scenarios discussed  
175 below (data not shown).



176

177 *Figure 1: Estimated inter-tactical genetic correlation for a quantitative trait dependent on its heritability, in the case of an*  
 178 *autosomal ART locus. Error bars denote 95% confidence intervals and points are jittered to avoid overlap. Estimates*  
 179 *increase with increasing heritability. Increasing the magnitude of the difference between ARTs (here by a factor of two)*  
 180 *does not affect the estimated genetic correlation. However, reducing the offspring number within each family (by 50%*  
 181 *shown here) and a higher variance in one ART ( $SD\ ART1 = 2 * SD\ ART2$  shown here) both decrease the magnitude of the*  
 182 *estimated genetic correlation. Points falling above the dashed 1:1 line have a higher estimated genetic correlation than the*  
 183 *heritability of the trait.*

## 184 Sex-linked ART locus

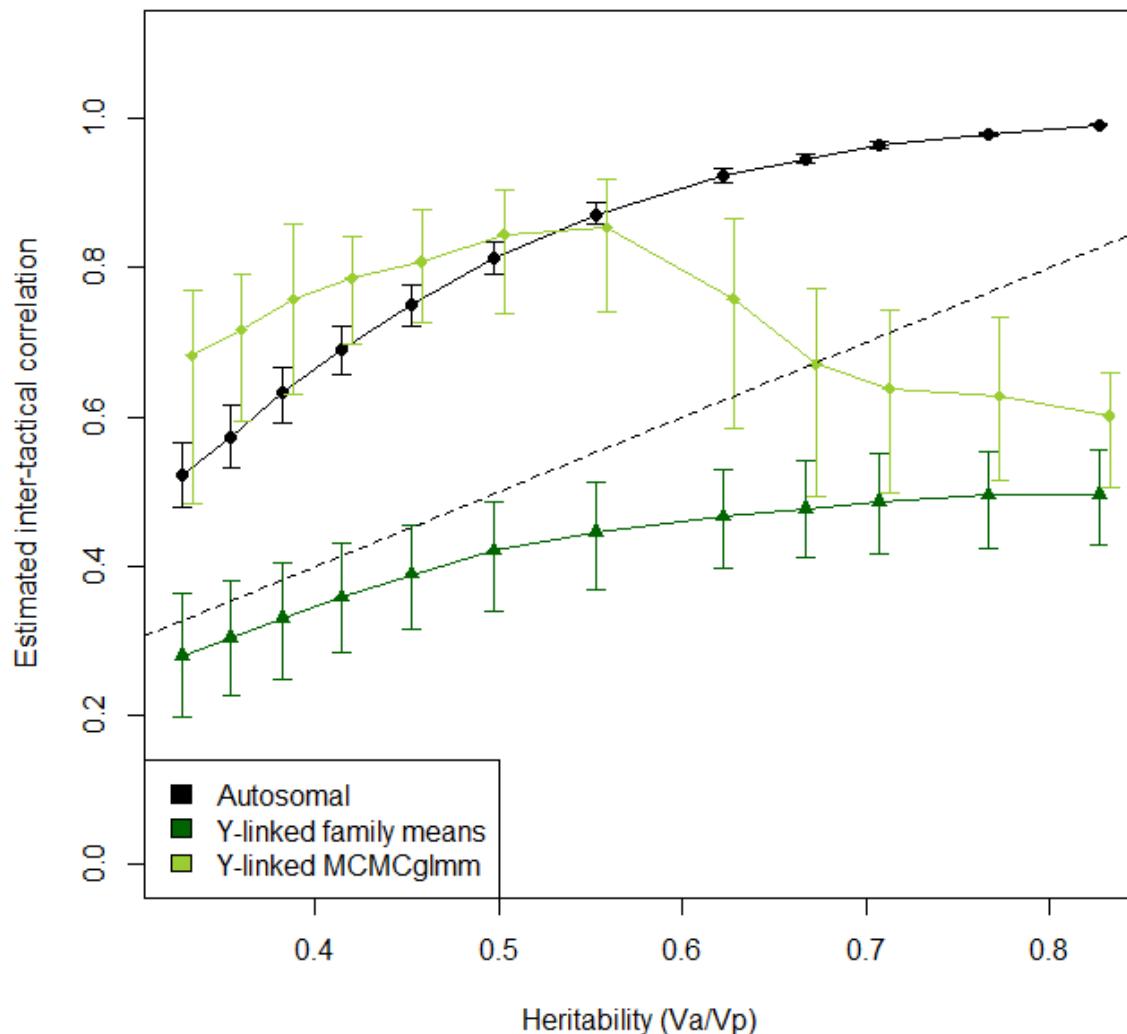
185 We assume XY sex determination for simplicity, but the results of these simulations should be  
 186 equally applicable to species with ZW sex determination. In the case of X-linkage, the results are the  
 187 same as for an autosomal ART locus, as long as it is possible to produce families with a mix of ARTs.  
 188 For a male-limited X-linked polymorphism, heterozygote female carriers will produce mixed broods,  
 189 and for a dominant female-limited X-linked polymorphism, mixed broods can be produced either by  
 190 heterozygote mothers mating males carrying the recessive allele, or by homozygote mothers who

191 mate with males carrying the opposite allele. Given that we assume that the trait and the morph  
192 locus are unlinked, results for an X-linked locus are therefore the same as for an autosomal locus  
193 since an individual's morph assignment is independent of its breeding value for the trait. In practice,  
194 estimates will probably often be lower for X-linked loci compared to autosomal loci because of the  
195 difficulty in obtaining large numbers of offspring of each ART from the same family (Figure 1).

196 For a Y-linked locus, it will never be possible to produce full siblings of different ARTs, which means  
197 that some sort of maternal half-sib design is necessary for estimating inter-tactical genetic  
198 correlations. We therefore assumed a design where each mother is mated to two males, one from  
199 each ART. In this case, the family means method of estimation will consistently underestimate the  
200 genetic correlation due to the lower level of relatedness between siblings of different ARTs, so we  
201 also analysed simulated Y-linked datasets using MCMCglmm (Hadfield 2010). MCMCglmm analyses  
202 were run with a modified inverse Wishart prior, and assume that 50% of the variance in the trait is  
203 genetic in origin (Mousseau and Roff 1987). The number of iterations was 11000 with a burn-in  
204 period of 1000 and thinning interval of 50. This produced a reasonable autocorrelation in the trial  
205 runs that were carried out. The effective sample size is rather small with this combination of  
206 parameters, but was retained in the interest of saving time. Because MCMCglmm analyses are  
207 considerably more time-consuming to run than calculating the correlation based on family means  
208 (since each run involves a large number of permutations), the MCMCglmm analyses were carried out  
209 on 50 simulated datasets for each parameter combination, instead of 1000, resulting in wider  
210 confidence intervals for the MCMCglmm estimated compared to the family means estimates (Figure  
211 2).

212 As expected, uncorrected inter-tactical correlations estimated from family means were about half  
213 the magnitude for Y-linked tactics compared to autosomal ones, due to the half-sib breeding design.  
214 Although accuracy of the estimates can be improved by multiplying the calculated correlation by two  
215 to take reduced relatedness into account, precision will still be considerably lower (i.e. high  
216 confidence intervals) for Y-linked tactics compared to autosomal tactics. The MCMCglmm analysis  
217 was more effective in producing estimates for Y-linked tactics that were similar to those for an  
218 autosomal locus, at least for lower heritability values (Figure 2). The decrease in estimates at high  
219 heritabilities ( $>0.6$ ) is likely a side effect of the prior which assumes a heritability of 0.5. This suggests  
220 that unless information about the heritability of the quantitative trait is incorporated into the  
221 analysis, intertactical genetic correlations may be inaccurately estimated even when using  
222 MCMCglmm.





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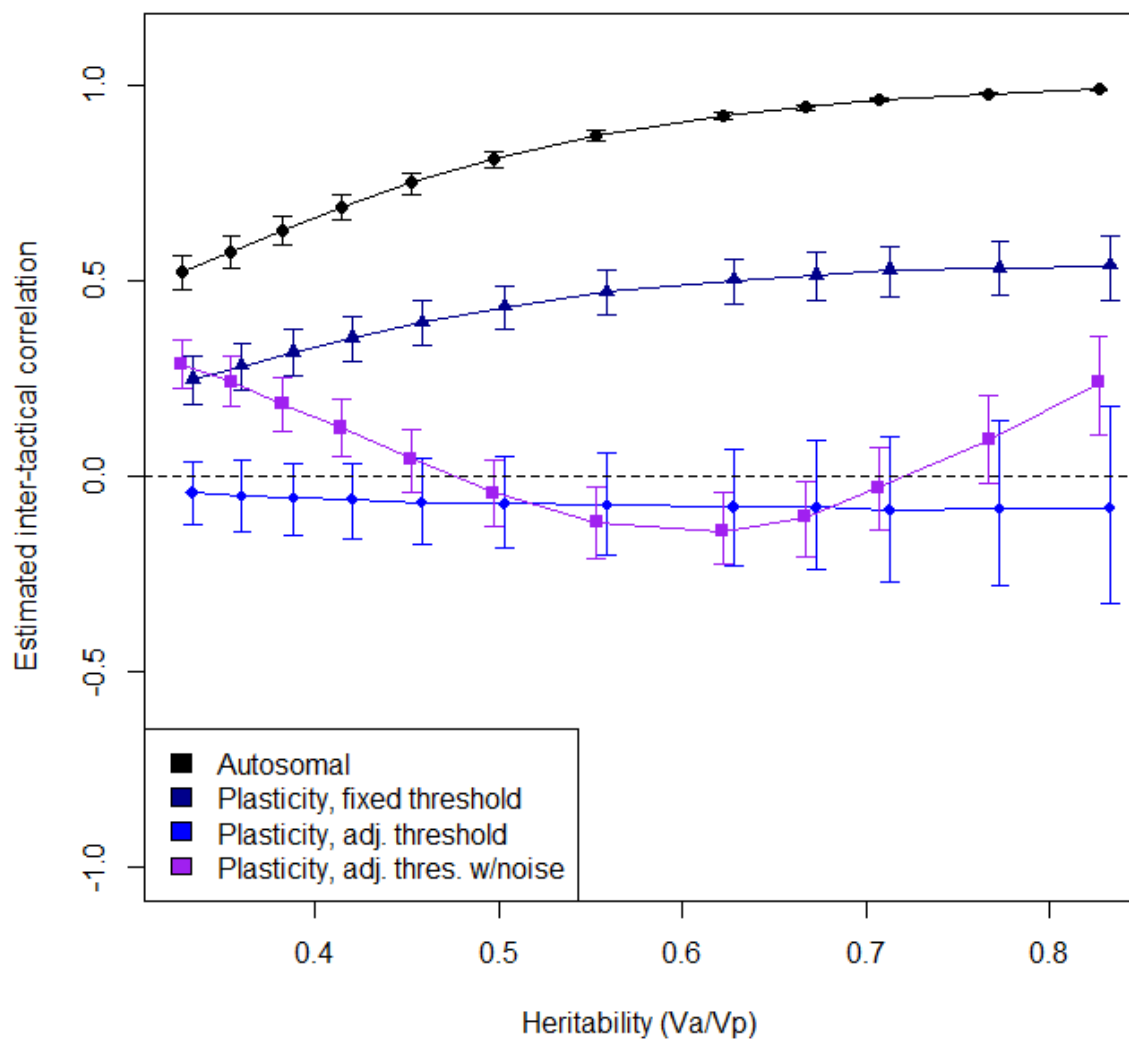
224 *Figure 2: Estimated inter-tactical genetic correlation for a quantitative trait dependent on its heritability, in the case of a Y-*  
 225 *linked ART locus. Baseline values for the autosomal case are included for the sake of comparison. Error bars denote 95%*  
 226 *confidence intervals and points are jittered to avoid overlap. Raw family means values are approximately half that of the*  
 227 *autosomal case, and confidence intervals are wider. MCMCglimm performs well when the prior accurately reflects the true*  
 228 *additive genetic variance (see main text for details). Points falling above the dashed 1:1 line have a higher estimated*  
 229 *genetic correlation than the heritability of the trait.*

230

## 231 Developmentally plastic ARTs

232 In the case of developmentally plastic ARTs, which tactic an individual becomes is determined by a  
 233 phenotypic switching threshold. In many species, this is determined by body size, which is usually  
 234 heritable, but also tends to reflect overall condition. Following Buzatto *et al.* (2015), we assumed  
 235 that the switching threshold is genetically fixed in the population and the same as the population  
 236 mean. We also assumed that the trait that determines the switching threshold is also the one for

237 which we wish to estimate the intertactical genetic correlation. In practice, this means that only  
238 families with a breeding value relatively close to the population mean for the quantitative trait will  
239 produce offspring that belong to both ARTs, unless environmental manipulations make it possible to  
240 influence the developmental trajectory (we chose not to simulate this sort of manipulation for the  
241 sake of simplicity). We chose this approach because it is likely to be the least favourable scenario for  
242 detecting intertactical genetic correlations; if the trait of interest is not the



243

244 *Figure 3: Estimated inter-tactical genetic correlation for a quantitative trait dependent on its heritability, in the case of*  
245 *developmentally plastic ARTs. Baseline values for the autosomal case are included for the sake of comparison. Error bars*  
246 *denote 95% confidence intervals and points are jittered to avoid overlap. If the switching threshold is genetically fixed in the*  
247 *population, then estimates are lower and more variable overall, but follow a similar pattern as in the autosomal case. If*  
248 *there is genetic variation for the switching threshold, then estimates often include zero (indicated by the dashed line) even*  
249 *though the true underlying genetic architecture is a perfect correlation.*

250

251 trait that determines the switching threshold, then it should be much easier to obtain mixed  
252 families.

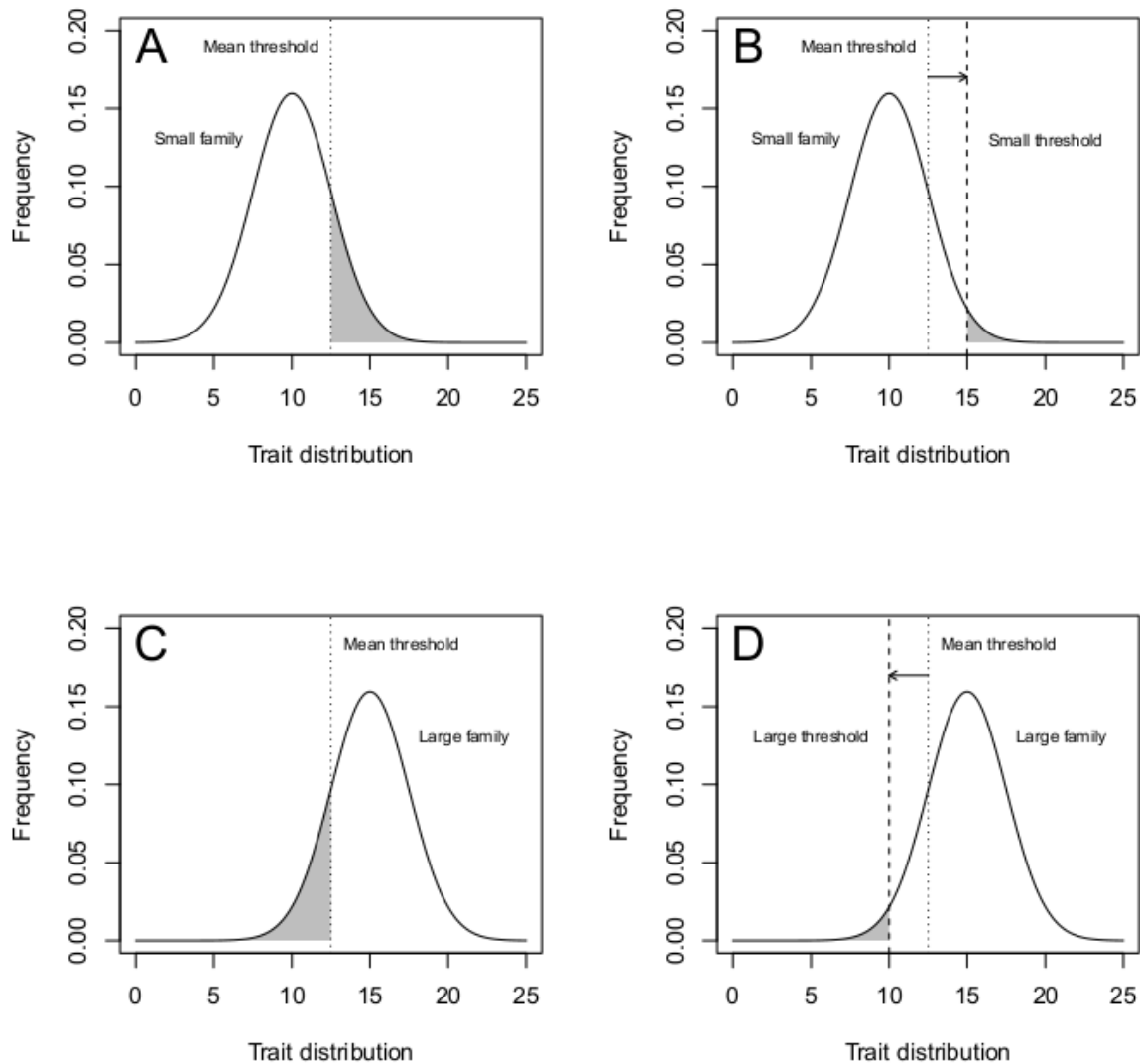
253 If we take body size as an example, then in this scenario, all males that are below the population  
254 mean body size at the developmental decision point become the “small” ART (i.e. sneaker or minor  
255 males) and all males that are above the population mean body size at the developmental decision  
256 point become the “large” ART (i.e. courter or major males). We found that the estimated inter-  
257 tactical genetic correlation is lower for developmentally plastic tactics compared to an autosomal  
258 ART locus, but that the estimates are still always significant as long as the heritability of the  
259 quantitative trait is moderately high ( $>0.3$ ; Figure 3, dark blue triangles). The confidence interval for  
260 the estimates is also higher, which is likely a result of decreased effective sample size since not all  
261 families will produce mixed broods.

262 We predict that under intra-locus tactical conflict, it would be advantageous for developmentally  
263 plastic ARTs to evolve the ability to adjust the switching threshold to match the value of the  
264 quantitative trait that determines the developmental trajectory. For example, a family with genes  
265 for becoming large will tend to produce particularly large “small” males, which may be inefficient at  
266 obtaining sneaky matings. Similarly, a family with genes for becoming small will tend to produce  
267 particularly small “large” males, which may likewise be inefficient at courting females. A family with  
268 genes for low values of the switching threshold trait should therefore adjust the threshold upwards  
269 if possible (Figure 4), and vice versa for families with high values of the trait.

270 There are multiple ways in which the switching threshold could be adjusted. We examine two main  
271 types of adjustment, including or excluding the effect of developmental noise. It is not our aim here  
272 to explore all possible means of adjusting the switching threshold – although there has been much  
273 speculation that species can harbour genetic variation in switching threshold, demonstrating that  
274 this is not trivial, since it requires raising similar genotypes across a range of environmental factors.  
275 This means that data on what sort of switching adjustment patterns may exist is sparse (Taborsky  
276 2017). We therefore chose to examine two simple types of adjustment scenarios to see if and how  
277 threshold adjustment can alter the estimate of the inter-tactical genetic correlation.

278 If developmental noise is not taken into account when adjusting the switching threshold, then a  
279 simple rule is to move the threshold upwards or downwards the same amount as the family  
280 deviation from the population mean. For example, a family with a breeding value 0.5 standard  
281 deviations above the mean would move its switching threshold to 0.5 standard deviations below the  
282 mean, ensuring that only individuals with a trait value that is 1 population standard deviation below  
283 the family mean will develop into the “small” tactic (Figure 4). We found that this type of adjustment

284 results in universally low and non-significant estimates of the inter-tactical genetic correlation, since  
 285 the adjustment cancels out the effect of underlying genetic differences in the quantitative trait  
 286 (Figure 3, light blue diamonds). Changing the magnitude of the adjustment (e.g. by multiplying the  
 287 family deviation from the population mean by a fixed constant) alters the slope of the relationship  
 288 between the estimate and  $V_a/V_p$ , but the general conclusions hold (Figure S1).



289  
 290 *Figure 4: In a family of small individuals, individuals above the switching threshold will develop as “large” (i.e.*  
 291 *major/courter, shaded area below the curve) males but be at the lower end of the size distribution for this ART (A). It would*  
 292 *therefore be potentially advantageous for males in this family to adjust their switching threshold upwards (B). Conversely,*  
 293 *in a family of large individuals, individuals below the switching threshold will develop as “small” (i.e. minor/sneaker, shaded*  
 294 *area below the curve) males but be at the higher end of the size distribution for this ART (C). It would therefore be*  
 295 *potentially advantageous for males in this family to adjust their switching threshold downwards (D). Figure partially*  
 296 *adapted from Buzatto et al. (2015).*

297

298 When developmental noise is not taken into account, as in the scenario above, this means that  
299 families with extreme values of the focal trait will not produce mixed broods unless the  
300 developmental noise parameter is very large. We therefore decided to explore what would happen if  
301 the switching threshold was adjusted relative to both the family breeding value and the degree of  
302 developmental noise. In this scenario, the threshold adjustment was scaled according to the  
303 developmental noise, such that a family with a breeding value 0.5 standard deviations above the  
304 population mean will move its threshold 0.5 within-family standard deviations (i.e. the  
305 developmental noise parameter) below the population mean. This means that the magnitude of the  
306 adjustment increases as the developmental noise increases, which we feel is a reasonable approach.  
307 The greater the uncertainty in offspring phenotype, the more scope for adjustment is needed. We  
308 found that this scenario caused estimates of the inter-tactical genetic correlation to fluctuate from  
309 negative to positive, depending on the heritability of the trait (Figure 3, purple squares). Again,  
310 changing the magnitude of the adjustment (e.g. by multiplying the threshold displacement from the  
311 family mean by a fixed constant) moves the location of the inflection point of the relationship  
312 between the estimate and  $V_a/V_p$ , but the general conclusions hold (Figure S2).

## 313 Conclusions

314 Genetic correlations across ARTs is an essential criterion for intralocus tactical conflict to be a  
315 constraint on the evolution of ARTs. Our results suggest that such conflict is possible for  
316 developmentally plastic tactics, which is consistent with the detection of genetic correlations in  
317 some recent studies (Pike et al. 2017; Buzatto et al. 2018). In addition, we suggest that different  
318 methods are needed to detect genetic correlations across developmentally plastic ARTs, and that  
319 even for genetically influenced ARTs, the methods that can be applied will determine the extent to  
320 which real genetic correlations can be detected.

321 Inter-tactical genetic correlations are potentially more difficult to measure in  
322 developmentally plastic ARTs, unless experimental manipulations of conditions influencing the  
323 switch are possible (e.g. rearing soapberry bugs under a wide range of food and conspecific density  
324 conditions that influence a wing polyphenism, Fawcett et al. 2018; manipulated pheromones in  
325 mites to produce high status scramblers and low status fighters, Michalczyk et al. 2018). Estimates of  
326 genetic correlations were also lower for developmentally plastic tactics (at least using the family  
327 means method), meaning that non-significant results might be likely even if there is a true  
328 correlation. If there is an ability to adjust the switching threshold, all estimates become suspect.  
329 Plausible adjustment mechanisms include thresholds that are regulated by transcriptional switches.  
330 Gene-expression differences associated with polyphenic morphs have provided evidence for

331 transcriptional switches, e.g. differences in the expression of genes encoding insulin signaling  
332 components, which alters the reaction norm for the influence of nutrition on a wing polyphenism in  
333 the soapberry bug (Fawcett et al. 2018), and additional studies reviewed by Projecto-Garcia et al.  
334 (2017). In the case of male-limited ARTs, the maternal focal trait value could also be a source of  
335 information about the family breeding value. This means that phenotypic and maternal effects cues  
336 could be combined to decide how to adjust the switching threshold (McNamara et al. 2016). Finally,  
337 in cases where the ARTs are Y-linked, half-sib breeding designs are necessary (as mixed families are  
338 not possible), and inter-tactical correlations estimated from family means will be more difficult to  
339 detect compared to the genetic correlations across autosomal tactics. In this case, experimental  
340 tests such as experimental evolution may be the only way to conclusively confirm or deny the  
341 existence of an inter-tactical genetic correlation.

342 In summary, substantial inter-tactical genetic correlations and therefore IATC are clearly  
343 possible for developmentally plastic tactics. However, the study of these correlations will require  
344 further understanding of both the genetic and environmental influences on the underlying  
345 thresholds.

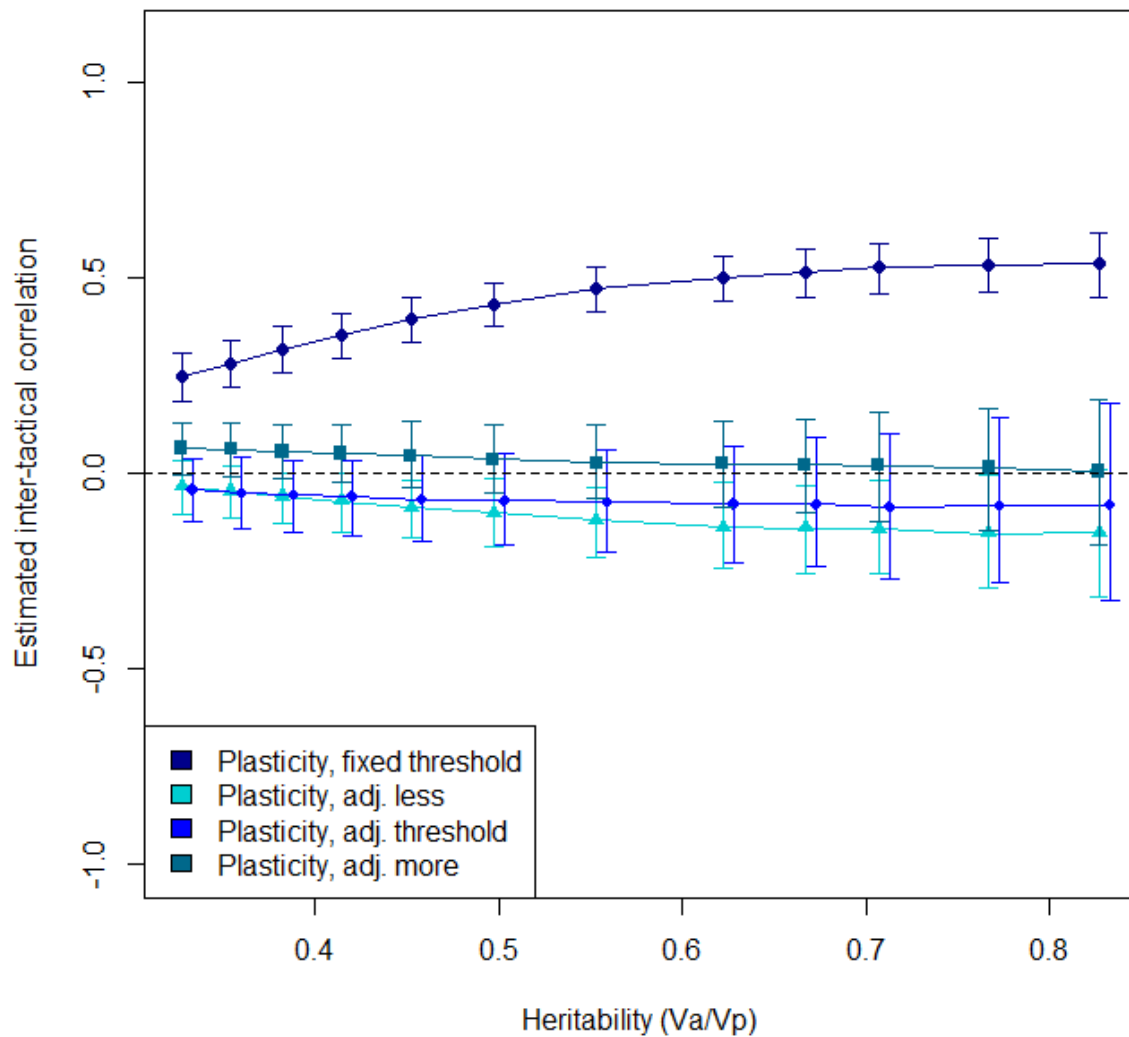
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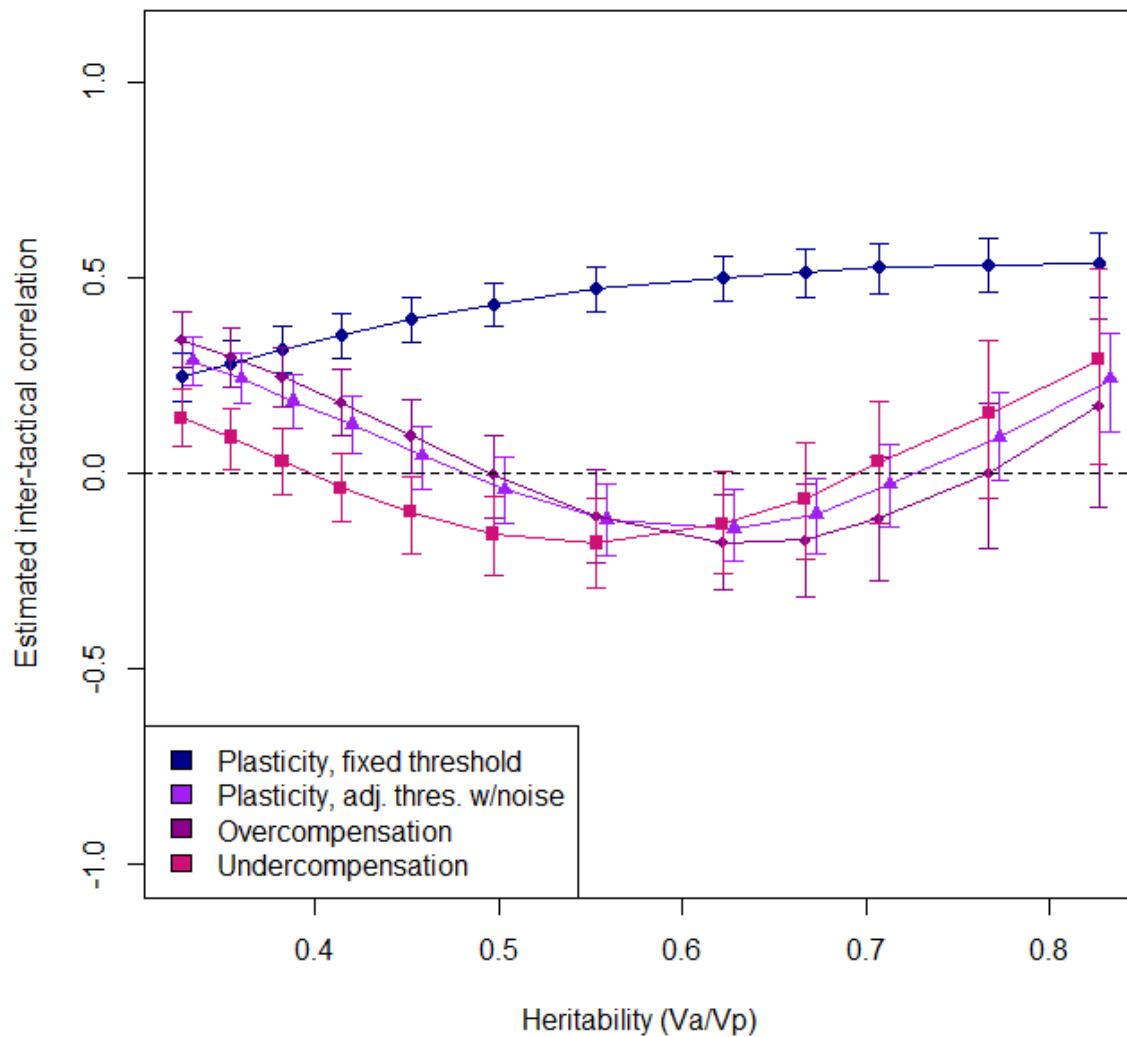
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422 *Figure S1: Estimated inter-tactical genetic correlation for a quantitative trait dependent on its heritability, in the case of*  
423 *developmentally plastic ARTs where development noise is not taken into account. Baseline values for the fixed switching*  
424 *threshold case are included for the sake of comparison. Error bars denote 95% confidence intervals and points are jittered*  
425 *to avoid overlap. Multiplying the adjustment value by a fixed constant (here 20% lower or higher, i.e. 0.8 and 1.2) changes*  
426 *the slope of the relationship but not the qualitative effect; estimated genetic correlations are still low and usually not*  
427 *significantly different from zero.*

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431 *Figure S2: Estimated inter-tactical genetic correlation for a quantitative trait dependent on its heritability, in the case of*  
432 *developmentally plastic ARTs where development noise is taken into account. Baseline values for the fixed switching*  
433 *threshold case are included for the sake of comparison. Error bars denote 95% confidence intervals and points are jittered*  
434 *to avoid overlap. Multiplying the adjustment value by a fixed constant (here 20% lower or higher, i.e. 0.8 and 1.2) changes*  
435 *the inflection point but not the qualitative effect; estimated genetic correlations are still low and point estimates vary from*  
436 *negative to positive depending on the heritability of the trait.*

