

1 *PHIL TRANS SPECIAL ISSUE:*  
2 *The role of plasticity in phenotypic adaptation to rapid environmental change*

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4 **Sexual selection, phenotypic plasticity, and female reproductive output**

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15  
16 **Keywords:** adaptation, condition-dependence, environmental change, fitness, genetic  
17 correlation, trade-offs.

18  
19 **Summary**

20  
21 In a rapidly changing environment, does sexual selection on males elevate a population's  
22 reproductive output? If so, does phenotypic plasticity enhance or diminish any such effect?  
23 We outline two routes by which sexual selection can influence the reproductive output of a  
24 population: a genetic correlation between male sexual competitiveness and female lifetime  
25 reproductive success; and direct effects of males on females' breeding success. We then  
26 discuss how phenotypic plasticity of sexually selected male traits and/or female responses  
27 (e.g. plasticity in mate choice), as the environment changes, might influence how sexual  
28 selection affects a population's reproductive output. Two key points emerge. First, condition-  
29 dependent expression of male sexual traits makes it likely that sexual selection increases  
30 female fitness *if* reproductively successful males disproportionately transfer genes that are  
31 under natural selection in both sexes, such as genes for foraging efficiency. Condition-  
32 dependence is a form of phenotypic plasticity if some of the variation in net resource  
33 acquisition and assimilation is attributable to the environment rather than solely genetic in  
34 origin. Second, the optimal allocation of resources into different condition-dependent traits  
35 depends on their marginal fitness gains. As male condition improves, this can therefore  
36 increase or, though rarely highlighted, actually decrease the expression of sexually selected  
37 traits. It is therefore crucial to understand how condition determines male allocation of  
38 resources to different sexually selected traits that vary in their immediate effects on female  
39 reproductive output (e.g. ornaments versus coercive behaviour). In addition, changes in the  
40 distribution of condition among males as the environment shifts could reduce phenotypic  
41 variance in certain male traits, thereby reducing the strength of sexual selection imposed by  
42 females. Studies of adaptive evolution under rapid environmental change should consider the  
43 possibility that phenotypic plasticity of sexually selected male traits, even if it elevates male  
44 fitness, could have a negative effect on female reproductive output, thereby increasing the  
45 risk of population extinction.

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## 50 1. Introduction

51

52 Sexual selection favours traits that are often exclusively expressed or only exaggerated in  
53 males, such as weapons and ornaments, which increase mating or fertilization success when  
54 there is competition for mates or fertilization opportunities. In contrast, natural selection  
55 favours economically efficient traits that are usually similarly expressed in both sexes, which  
56 improve foraging ability, predator evasion, disease resistance and so on. In general, therefore,  
57 natural and sexual selection are in opposition. There is a trade-off between a longer life or a  
58 faster mating rate (but see [1,2]). It might therefore seem slightly paradoxical that researchers  
59 have asked whether sexual selection on males can increase the rate at which females adapt to  
60 a novel environment [3-7]. This is akin to asking if sexual selection on *males* elevates the  
61 mean absolute lifetime reproductive output of *females* (i.e. population mean fitness  
62 [definition modified from 8; see also 9]), thereby increasing the maximum population growth  
63 rate and decreasing the likelihood of population extinction. In a similar vein, researchers  
64 studying phenotypic plasticity, especially those motivated by conservation concerns arising  
65 from climate change, industrial-scale agriculture and urbanization, have asked whether plastic  
66 responses to rapid environmental change reduce the likelihood of population extinction  
67 ('plastic rescue' *sensu* [8]) because phenotypic plasticity increases population mean fitness  
68 [10].

69

70 Surprisingly, these two research questions are rarely combined. Researchers studying plastic  
71 rescue mostly ask whether plastic responses of naturally selected traits to a changing  
72 environment are broadly adaptive (i.e. elevate male and female absolute fitness). It is rare for  
73 them to instead ask whether adaptive plasticity of sexually selected traits in *males* (i.e. those  
74 that increase relative mating or fertilization success) will increase the mean absolute lifetime

75 reproductive output of *females*. Before proceeding further, we should acknowledge that mean  
76 *female* lifetime reproductive success (LRS) is an imperfect proxy for the realised growth of a  
77 population and its effective population size (the two key demographic parameters that  
78 influence extinction risk [review: 11; see also 12]). We are essentially assuming there is  
79 ‘hard’ rather than ‘soft’ selection on female LRS [see 13] such that *absolute* differences in  
80 female LRS between a population with and without sexual selection translate into differential  
81 recruitment rates. This is a simplification, but one that is widely used when investigating so-  
82 called ‘population fitness’ [e.g. 8].

83

84 Many factors select for different levels of expression of sexually selected traits by males  
85 [review: 14]. For example, the sonic and light environment affect the transmission of acoustic  
86 and visual courtship signals respectively [review: 15]; and the local predator and parasite  
87 community determine the costs of investing in attractive traits that increase a male’s  
88 vulnerability to predators, or capacity to tolerate parasites. The benefits of investing in  
89 sexually rather than naturally selected traits also depend on the strength of sexual selection,  
90 which can covary with the operational sex ratio, density of competitors and mate encounter  
91 rate [16-18]. Perhaps the most important and widespread form of phenotypic plasticity in  
92 sexually selected traits relates to the availability of resources. Many sexually selected traits  
93 show ‘condition-dependent’ expression, being smaller when food is limited. All of these  
94 factors should select for males that detect appropriate environmental cues and show an  
95 adaptive plastic response in their investment into sexually selected traits.

96

97 In this review, we explore how plastic responses by males to a changing/novel environment  
98 could influence the mean absolute lifetime reproductive success (LRS) of females, hence the  
99 likelihood of population extinction. We focus on plasticity in males rather than females

100 because theory suggests that sexual selection mainly acts on males [19-21]. This claim is  
101 widely supported empirically by greater male weaponry and ornamentation [22-25], and by a  
102 stronger relationship in males than females between mating and reproductive success [26; but  
103 see 27-28] (for examples of sexual selection in females see [29, 30]).

104

105 (Terminology: We define *phenotypic plasticity* as a genotype producing different phenotypes  
106 depending on the environment in which it is expressed. This is broadly synonymous with  
107 individuals (whose genotype is constant) showing a *plastic response*. The response is  
108 adaptive if it increases fitness compared to continued expression of the phenotype produced  
109 prior to the environmental change of interest. When referring to the degree of plasticity  
110 expressed by a genotype we refer to its *reaction norm* (the function relating the expression of  
111 the focal trait to an environmental parameter). Selection for an adaptive plastic response is  
112 synonymous with selection for an appropriately shaped reaction norm. Evolution of plasticity  
113 can only occur if there is additive genetic variation in reaction norms (i.e. gene-by-  
114 environment [GxE] effects). We should note that individual plasticity is not strictly  
115 synonymous with GxE, despite individuals having different genotypes, because individuals  
116 might vary phenotypically across focal environments for purely non-genetic reasons (e.g. a  
117 good start in life might increase their ability to adjust their phenotype [permanent  
118 environment effects: see 31]).

119

## 120 **2. How can sexual selection affect female reproductive output?**

121

122 Regardless of whether or not phenotypic plasticity in sexually selected traits is adaptive for  
123 males, it seems unlikely on the face of it to affect the likelihood of population extinction in a  
124 rapidly changing environment. This is because the expression of sexually selected traits

125 simply determines which males mate. *Does this have any bearing on how many females there*  
126 *are, how often they breed, and the success of each breeding attempt?* Sexual selection on  
127 males will only influence population extinction if it affects these three key demographic  
128 parameters. We therefore first address the role of sexual selection in determining female LRS  
129 before we consider additional compounding effects of male plasticity. Naïvely we might  
130 assume that males cannot affect mean female LRS because females are rarely limited in their  
131 ability to acquire a mate, but this conclusion would be wrong [32]. Males can affect mean  
132 female LRS for three main reasons.

133

134 (a) There is a positive genetic correlation because successful males transfer genes that elevate  
135 their daughters' LRS ( $r_G$ ) [33,34]. This is most likely to occur when there is additive genetic  
136 variation for naturally selected genes that determine condition, and male sexual traits are  
137 condition-dependent (see §4). Conversely, there could be a negative correlation if successful  
138 males transfer sexually antagonistic genes that elevate their sons' mating success but lower  
139 their daughters' LRS [35,36]. A negative inter-sex genetic correlation ( $r_{MF}$ ) for fitness has  
140 been documented in several species [37-41], but this is not strictly equivalent to a negative  
141 genetic correlation between male sexual competitiveness and female LRS. For example, even  
142 in the absence of sexual selection, a negative  $r_{MF}$  could arise if natural selection favours  
143 different genotypes in each sex, which is likely given sex-specific life histories [e.g. 42-44].  
144 Strictly speaking it is necessary to measure the genetic correlation ( $r_G$ ) between male and  
145 female fitness that is attributable to sexual and natural selection respectively. This correlation  
146 is likely to vary predictably depending on the environment in which it is measured  
147 [45,46](see §5). It should also be noted that a positive  $r_G$  is not equivalent to female choice  
148 for genetic quality ('good genes'), as this refers to a sire's effect on mean offspring fitness  
149 (i.e. daughters *and* sons) [47-49].

150

151 (b) There is a phenotypic correlation ( $r_P$ ), between a male's mating success and his mate's  
152 LRS because male sexual competitiveness covaries with: (i) traits that determine the level of  
153 sexual conflict over mating and sperm use (e.g. seminal toxins, traumatic damage to females)  
154 [50-52]; (ii) the likelihood he passes on sexually transmitted infections [53,54]; (iii) the  
155 quantity and/or quality of resources transferred (e.g. parental care, nuptial gifts) that improve  
156 a female's ability to rear viable offspring [55-57]; and, (iv) his daughters' LRS due to his rate  
157 of 'offspring provisioning' (e.g. food intake when young, or access to breeding resources as  
158 an adult) [e.g. 58,59]. When calculating the contribution of successful males to a population's  
159 reproductive output we need to determine how many daughters they sire compared to the  
160 average male, and if their daughters are of above average fecundity [60]. In general, however,  
161 there is only weak empirical evidence that sire attractiveness affects the offspring sex ratio  
162 [61].

163

164 (c) Even if we ignore the issues of which males mate, male-male competition leads to the  
165 coevolution of sexually selected male traits and corresponding female traits (e.g. mate choice,  
166 mating resistance), that generally reduce female LRS below the level that would occur in  
167 their absence [62]. First, investment into sexual traits lowers males' parental investment,  
168 reducing the mean output per breeding event [21]. Second, intense sperm competition can  
169 cause sperm depletion that lowers fertilization success, reducing the output per breeding  
170 event. This is most common when only a subset of males acquire mates [63,64]. Third, sexual  
171 conflict that arises when female evade and resist males tends to increase the interval between  
172 breeding events, and lowers female fecundity due to energetic costs, lost foraging time and  
173 allocation of resources to defensive traits instead of offspring [65-67]. Sexual conflict can  
174 also kill females, reducing the number of breeding females in a population [68,69].

175

176 **3. The net effect of sexual selection on mean female reproductive output**

177

178 For all of the scenarios covered in §2a,b there are both theoretical models and empirical data  
179 suggesting that mating with more successful (i.e. competitive) males can have either a  
180 positive or negative effect on mean female LRS, depending on contingent factors. For  
181 example, the proportion of genes with sexually antagonistic effects tends to be lower when  
182 populations are in a novel or changing environment [e.g. 70-72] (§5). Consequently, there is  
183 no consensus as to how variation in male mating success due to sexual selection affects the  
184 likelihood of population extinction. In contrast, all of the sexually selected processes in §2c  
185 reduce mean female LRS. The net effect of sexual selection on mean female LRS, hence  
186 population extinction risk, is therefore uncertain [3-7], although it seems on balance to be  
187 beneficial.

188

189 First, sexual selection is positively correlated with lineage diversification (speciation minus  
190 extinction rates) across many taxa [73,74; but see 75,76]. If this relationship is partly driven  
191 by lower extinction rates, it is plausible that sexual selection has a beneficial effect on mean  
192 female LRS. Second, a recent study of ostracods found that persistence in the fossil record  
193 (i.e. time to extinction) was shorter for species assumed to have more intense sexual selection  
194 on males [77]. Third, numerous experimental evolution studies have created breeding lines in  
195 which sexual selection is either present (females have access to many males) or absent  
196 (enforced monogamy). The two types of lines often evolve differences in female fecundity,  
197 lifespan, offspring viability and other traits [review: 78]. Sexual selection clearly elevates  
198 components of female LRS in some studies [e.g. 79-81] but not others [e.g. 82-84].

199 Intriguingly, a few studies have directly shown that sexual selection lowers the rate of line  
200 extinction [85-88].

201

#### 202 **4. Environmental drivers of plasticity in sexually selected male traits**

203

204 In §2 we noted that sexually selected male traits can vary in the costs they impose on female  
205 LRS (e.g. ornaments versus seminal toxins). A key challenge in understanding how plasticity  
206 affects population extinction risk is therefore to predict how males plastically allocate  
207 resources into different sexually selected traits as the environment changes. We defer  
208 discussion of this topic to §6. In this section, we simply introduce three key factors that  
209 induce plasticity in sexually selected traits: environment-dependent resource availability, the  
210 social environment, and the signalling environment. We emphasise the benefits to males of  
211 these plastic responses with the implicit understanding that whether they are adaptive or not  
212 also depends on the costs of developmental/cognitive mechanisms that allow for plasticity,  
213 the capacity to detect environmental cues, and the likelihood of misinterpreting these cues  
214 [89-92]. See [10] for a more complete discussion of the costs of plasticity in the context of  
215 adaptation to novel environments.

216

#### 217 *Condition-dependence traits: a plastic response to resource availability*

218

219 ‘Condition’ is defined as the acquired resources that an individual can strategically allocate to  
220 life history traits [93]. Condition is a simple concept invoked in numerous sexual selection  
221 models [49; 94,95], but it is notoriously difficult to measure [96,97]. Nonetheless, it is often  
222 stated that most sexually selected traits are strongly condition-dependent [98-100]. This claim  
223 is based on trait expression positively covarying with environmental variation in resource



224 availability, and this covariation being stronger for sexually than naturally selected traits  
225 [97,101] (e.g. a greater change in sexually than naturally selected traits when diet is  
226 manipulated). It remains unclear to us whether other key life history traits (e.g.  
227 immunocompetence, female fecundity) are, in fact, less condition-dependent than sexually  
228 selected male traits [review by 98; but see 99,102]. Nonetheless, phenotypic plasticity in  
229 sexually selected traits attributable to environmental variation in resource availability is often  
230 high. This is consistent with a zero-sum game in which success at competing for mates and  
231 eggs is largely determined by a male's relative investment in attractiveness, fighting ability  
232 and sperm competitiveness [103,104].

233

234 Variation in condition among individuals arises due to contingent external factors (e.g. season  
235 of birth that affects resource availability in the environment) and direct effects of many  
236 naturally selected traits that determine the ability to acquire or assimilate resources (e.g.  
237 foraging ability, immune function). Strictly speaking we cannot treat condition-dependence  
238 as synonymous with phenotypic plasticity. Why? Plasticity involves a change in trait  
239 expression for a given genotype due to the environment. In contrast, condition-dependence  
240 could reflect differences in the resources that can be allocated to a trait that arise solely from  
241 genetic differences among individuals rather than environmental factors. However, we think  
242 it is biological sensible to assume that phenotypic variation in condition-dependence traits  
243 arises due to both genetic and environmental variation. In addition, we assume that condition-  
244 dependence is almost always associated with GxE interactions (hence additive genetic  
245 variation in reaction norms) when considering large environmental changes because when the  
246 environment changes in unexpected directions it seems likely that only some of the existing  
247 standing genetic variation will yield phenotypes that improve an individual's fit to the  
248 environment and thereby increase condition.

249 Crucially, variation in condition among males is ‘revealed’ in condition-dependent, sexually  
250 selected traits. So male mating success is potentially correlated with additive genetic  
251 variation for naturally selected traits that benefit females, thereby making  $r_G$  positive if  
252 condition-enhancing genes elevate both male mating success and female LRS. Phrased  
253 slightly differently, condition-dependent traits provide a mechanism whereby sexual selection  
254 can eliminate deleterious alleles from a population, regardless of whether they arise due to  
255 mutations, gene flow between locally adapted populations [13,105,106], or mismatch due to  
256 environmental change [5,107; but see 108]. The existence of condition-dependent, sexually  
257 selected male traits might therefore seem likely to elevate mean female LRS because of the  
258 genetic benefits to females of mating with males in good condition. Unfortunately, this  
259 conclusion is premature because many condition-dependent traits also damage females as a  
260 by-product of conferring an advantage to males when there is sexual conflict over mating  
261 (e.g. [109]). This makes it crucial to know how males allocate resources to different  
262 condition-dependent traits as resource availability changes due to the environment (see §6).

263

#### 264 ***The social environment: the response to cues of sexual competition***

265

266 Males could benefit from plastic responses of sexually selected traits to the number of  
267 competitors, the sex ratio, and other social factors that affect the compound probability of  
268 obtaining a mate and their sperm achieving fertilization. The most common plastic responses  
269 are shifts in sperm production, ejaculate size, and rates of courtship or aggression [63, 110-  
270 114]. Studies that examine plastic responses to the social environment by males rarely  
271 quantify the effect on female reproductive output [115,116; but see 117]. Instead, researchers  
272 usually extrapolate from effects of male traits on females in other studies to predict how male  
273 plasticity will alter female LRS. For example, male *Drosophila* that perceive higher rates of

274 sperm competition mate for longer and stimulate higher rates of egg laying [118]. All else  
275 being equal, this implies that male plasticity might elevate female LRS, but this is obviously  
276 contingent on the mortality costs to females of a male-induced increase in productivity [e.g.  
277 119]. In other studies, male plasticity seems likely to reduce female LRS. For example,  
278 dominant males in domestic fowl mate more often and produce more sperm than subordinates  
279 but, unlike subordinates, ejaculate quality decreases over successive copulations [120].  
280 Greater investment into sperm in a more competitive social environment could therefore  
281 lower female LRS if it reduces egg fertilization rates.

282

283 Our understanding of how plastic response of males to social cues affect female LRS is  
284 limited. In some cases, we can use theory to reliably predict plastic responses in specific male  
285 traits (e.g. strategic ejaculation [113]). In other cases, the plastic response is not in the  
286 predicted direction. For example, there were no consistent effects of perceived future mating  
287 opportunities on investment into either pre or post-copulatory sexual traits by guppies [121];  
288 nor did male mice adjust their ejaculates to the number of potential mating opportunities,  
289 although they did so in response to the perceived risk of sperm competition [122]. These  
290 anomalies might arise because the marginal benefits of allocating resources to different  
291 sexually selected traits depend on the level of mating and fertilization competition [114].  
292 Again, this means it is crucial to be able to predict how males allocate resources to different  
293 traits if we want to relate male plasticity to female LRS (§6).

294

### 295 *The signaling environment*

296

297 There is good evidence, especially in species where males call to attract females, that males  
298 adjust their signals to the transmission properties of the environment. These are often

299 textbook examples of adaptive plasticity. For example, studies show that anthropogenic  
300 factors, such as urban noise and artificial lighting, impose direct selection on sexually  
301 selected male traits [123,124]. Numerous studies have further reported differences between  
302 urban and rural populations in sexually selected traits, such as bird song [125,126; review:  
303 127]. Many of these differences are in the direction predicted by functional considerations  
304 about signal transmission efficacy [128]. It seems improbable that selection on male genetic  
305 variation in song imposed by urban noise is responsible for urban-rural population differences  
306 [but see 129]. Given the recent origin of cities, these differences instead implicate plastic  
307 responses due to learning, and even cultural evolution. In general, it seems unlikely that male  
308 plasticity in response to the signaling environment will affect mean female LRS. It might,  
309 however, reduce female mate search costs by increasing males' conspicuousness; and it could  
310 make it easier to discriminate between potential mates, which would increase the strength of  
311 sexual selection which can then affect female LRS (§5).

312

### 313 **5. Male plasticity and female reproductive output due to the genetic correlation ( $r_G$ )**

314 So far, we have broadly discussed how sexual selection might affect female LRS (§2,3), and  
315 then described the main types of plastic responses of male sexual traits (§4). Next, we ask  
316 how male plasticity affects mean female LRS, hence population extinction (§1), driven by the  
317 genetic correlation ( $r_G$ ) between non-random male mating success due to the expression of  
318 sexually selected traits and female LRS. We mainly emphasise the role of condition-  
319 dependence (i.e. plasticity when due to the environment) in male sexually selected traits.

320 In general terms the observed phenotypic response to selection ( $R$ ) of a trait in a two-trait  
321 system is:

$$322 \quad R_x = h_x^2 S_x + r_{xy} h_x h_y S_y \quad (1)$$

323

324 where  $h^2 = V_A/V_{Phenotype}$  = heritability,  $S$  = selection differential

325

326 Here we can think of  $x$  = female LRS,  $y$  = male mating success, so  $r_{xy} = r_G$  [equations 11.6  
327 and 19.3 in 130]. If the genetic correlation ( $r_G$ ) between female LRS and male sexual  
328 competitiveness is positive then non-random mating due to sexual selection on males hastens  
329 the fixation of genes that improve female LRS above that due to natural selection on female  
330 LRS. The magnitude of  $r_G$  depends on the additive genetic variation ( $V_A$ ) in male mating  
331 success and female LRS and their covariation ( $r = \text{covar}(x,y)/\sqrt{\text{var}(x)\text{var}(y)}$ ), while the  
332 correlated response to selection on male mating success on female LRS due to a non-zero  $r_G$   
333 also depends on the heritability of male mating success. If sexual selection is weak (i.e.  
334 variation in mating success is mainly due to chance) then there is little difference between  
335 mean male mating success and the mating success of those males that breed, so  $S$  for mating  
336 success is small; and the heritability of male mating success is also low because there is no  
337 effect of genetic variation in sexual competitiveness on male mating success. In the absence  
338 of sexual selection, a positive  $r_G$  has no effect on female LRS. Simply put, if females mate  
339 randomly they do not disproportionately mate with males with genes that elevate female  
340 LRS, even if  $r_G = 1$ .

341

342 Given condition-dependent expression of sexually selected male traits, theory suggests that  $r_G$   
343 is more positive in a novel or rapidly changing environment, as both sexes tend to have  
344 phenotypes that are similarly displaced from their selected optima (Fig. 1a). Genes under  
345 natural selection in males are therefore likely to benefit females because they will equally  
346 move females towards their new optimum. If so, the inter-sex genetic correlation for fitness  
347 ( $r_{MF}$ ) is positive [45,46]. More specifically for  $r_G$ , some of the  $V_A$  in condition-dependent,  
348 sexually selected male traits that determine male success is due to genes that otherwise

349 improve naturally selected traits (§4). As such, more competitive males carry genes that tend  
350 to elevate mean female LRS if natural selection acts concordantly on both sexes, hence  $r_G >$   
351 0. In contrast, in a stable environment, genes that are under consistent selection in both males  
352 and females (e.g. genes for condition) tend to reach fixation. The  $V_A$  in condition is then  
353 reduced so that a greater proportion of the standing additive genetic variation in LRS and  
354 male mating success is attributable to sexually antagonistic genes, hence  $r_G < 0$ . Studies that  
355 compare  $r_{MF}$  (often, but not always, identical to  $r_G$ ; see §2) between populations which are  
356 either well or poorly adapted to the local environment suggest that  $r_{MF}$  is more positive in  
357 novel environments [34,70,131]; but see [132-134], although a full meta-analysis is still  
358 needed. Of course, several key assumptions underlie the claim that  $r_G$  is more often positive  
359 in novel environments [34,46,108].

360

361 First, if additive genetic variance changes due to gene-by-environment (GxE) interactions  
362 [134] this can affect  $r_G$  or  $r_{MF}$  in unexpected ways. To take an extreme case,  $r_G = 0$  if there is  
363 no additive genetic variation in male mating success in a new environment where chance  
364 alone determines which males mate. For example, consider what happens in the case of a  
365 sexually dichromatic cichlid fish with female mate-choice based on male colour that lives in  
366 clear water if the environment becomes highly turbid [135-137]. Even if condition still  
367 determines male colouration, bright males do not have higher mating success and the link  
368 between condition, which still elevates female LRS, and male mating success is broken.

369 Second, sex-specific optima in a novel environment might be associated with greater intra-  
370 locus sexual conflict. For example, consider a population with a mean phenotype for a  
371 naturally selected trait that is intermediate between the male and female optima. A standard  
372 assumption is that, in the novel environment, the trait optima are displaced in the same  
373 direction for both sexes [138] (Fig. 1a). If, however, they are displaced in opposite directions

374 then the potential for intra-locus sexual conflict will increase (Fig. 1b; see also Fig.1 in 134]).  
375 Even if the new sex-specific optima are displaced in the same direction, if they are further  
376 apart in the novel environment then  $r_G$  will tend to be more negative once the population  
377 mean trait exceeds the new optimum of one sex (Fig. 1c). Third, even if sex-specific optima  
378 are minimally displaced, there could be greater sexual antagonism in a novel environment  
379 due to sex-specific GxE interactions. For example, a genotype beneficial to both sexes in the  
380 original environment could produce a phenotype that is displaced much further from the  
381 female than male optimum in the novel environment. This is plausible given that a novel  
382 environment might affect sex-specific life histories (i.e. the sexes differ more in the particular  
383 traits that increase their condition due to, for example, greater sex differences in the available  
384 prey types). The interested reader is referred to [108] for a useful summary of other ways in  
385 which  $r_{MF}$ ,  $r_G$  (and  $S$ ) might be affected by a changing environment.

386

387 So what role does male plasticity play in increasing the extent to which sexual selection on  
388 males increases female LRS in a novel environment? Unfortunately, most theoretical studies  
389 of how sexual selection facilitates adaptation implicitly assume that sexually selected traits  
390 are condition-dependent. This is because it is the only obvious mechanism to link the process  
391 of females disproportionately mating with males with greater investment in sexually selected  
392 traits (usually modelled assuming female choice) to genetic benefits that elevate female  
393 reproductive success [13,45,46,106]. However, this approach precludes answering the  
394 broader question of whether  $r_G$  is more positive, sexual trait heritability ( $h^2=V_A/V_P$ ) is higher,  
395 or  $S$  is larger in a novel environment if sexually selected traits are phenotypically plastic  
396 instead of fixed in expression (i.e. whether they increase the value of  $r_{xy}h_xh_yS_y$  in equation 1).  
397 We can, however, still ask how sexually selected male traits being condition-dependent might  
398 affect the values of these three key parameters when the environmental changes. It is worth

399 noting here that each of these terms incorporates elements of the other so they are not  
400 independent (e.g.  $V_A$  affects the value of  $r_G$  and  $h^2_{male\ mating}$ ; and  $h^2_{male\ mating}$  incorporates an  
401 element of  $S$ , i.e. if  $S = 0$  then  $h^2_{male\ mating} = 0$ )

402

### 403 *Plasticity and the heritability of male mating success*

404

405 Condition-dependence implies that the environment affects phenotypic variation in sexually  
406 selected male traits, hence sexual competitiveness, and mating success. The degree of  
407 phenotypic displacement of the average male from the naturally selected optimum in a novel  
408 environment is likely to affect the distribution of male condition, hence  $V_P$  [102, Fig.1 in  
409 134]. Males will generally be in poorer condition, and the resultant decline in mean condition  
410 is likely to be associated with greater variation in condition [see 108,139]. This implies that  
411 male mating success has lower heritability in a novel environment due to the larger  $V_P$ , but  
412 heritability ( $V_A/V_P$ ) also depends on  $V_A$ . Additive genetic variation in condition, hence sexual  
413 trait expression, is likely to change in unpredictable ways in a novel environment simply  
414 because of GxE interactions. This makes it unlikely that we can predict how condition-  
415 dependence will affect heritability. There is, however, some evidence from meta-analyses  
416 that heritability is lower in less favourable environments, although this is contingent on the  
417 type of trait being measured [140]. One explanation for lower heritability of condition in less  
418 favourable environments (i.e. when extractable resource availability is lower due to  
419 maladaptation) is that there is a minimum threshold below which individuals die, which  
420 reduces  $V_A$  for condition among surviving males.

421

### 422 *Plasticity and the strength of sexual selection*

423



424 The strength of sexual selection affects both  $S$  and  $h$  for mating success in equation (1). The  
425 heritability of male mating success depends on non-random variation in mating success due  
426 to sexual selection on males (because this creates the necessary link between  $V_A$  in male  
427 sexually selected traits and mating success). We therefore need to know how a novel  
428 environment changes the types of males that females choose, and what factors determine  
429 which males win fights, or have greater sperm competitiveness.

430

431 Initially, greater  $V_P$  for male condition in a novel environment seems likely to increase the  
432 strength of selection  $S$  because the contrast between high and low condition males is  
433 exacerbated. But this need not be the case. For example, the extent to which choosy females  
434 discriminate between males based on ornament size might decline when the mean ornament  
435 size is smaller due to males being maladapted and in poorer condition. This could occur if  
436 females use size-based threshold rules to determine which males are suitable mates: if most  
437 males fall below the threshold, they will be equally (un)attractive as mates. More generally,  
438 phenotypic variance in traits depends on how resources are allocated to different sexually and  
439 naturally selected traits. The relationship between the mean condition of males and how  
440 males allocate resources to different condition-dependent traits is hard to predict (§6). Plastic  
441 shifts in allocation, even if only among sexually selected traits, could lead to unexpected  
442 outcomes. These include males in better condition being less successful because plastic  
443 responses are maladaptive in the novel environment. This is plausible because these  
444 responses have evolved based on females' behaviour in the original environment. For  
445 example, greater investment into ejaculate size by males in better condition might be  
446 disadvantageous if females in a novel environment do not mate multiply. In sum, condition-  
447 dependent changes in allocation could alter  $V_P$  in key sexually selected traits in ways that  
448 change the proportion of variation in mating and fertilization success that is attributable to  $V_A$

449 in condition, thereby reducing the variation in male mating success that also increases female  
450 LRS. Similar adverse outcomes for female LRS could arise when males plastically respond to  
451 cues about the social, or even signalling, environment that alter covariation between  $V_A$  in  
452 condition and male mating success.

453

454 Another way that male plasticity could weaken sexual selection is if males respond to social  
455 cues by ‘specialising’ in increasing their success at certain stages of reproduction (e.g. mate  
456 acquisition versus fertilization). Here we note that, for ease, we previously treated sexual  
457 selection as synonymous with variation in mating success in equation 1. Strictly speaking we  
458 should refer to “variation in fertilization success which arises from the combined effects of  
459 female mate choice, cryptic choice, the intensity of sperm competition, and how winning  
460 male-male contests elevates mating and fertilisation success”. For brevity we do not.

461 Specialization can reduce variation in male reproductive success under sexual competition if  
462 males make the ‘best of a bad job’ (e.g. small males or those in low condition sneak rather  
463 than court [141]). More generally, when males plastically adjust their investment in sexually  
464 selected traits to take advantage of information about individual females, this can reduce  
465 variation in male fitness. For example, males can plastically adjust ejaculate size based on  
466 cues about a female’s previous mating history or the likelihood that she will re-mate [113].

467

468 Conversely, plasticity could increase  $V_P$  in male reproductive success under sexual  
469 competition. For example, a lack of detectable variation among males in one trait in a novel  
470 environment could favour females that shift their attention to assessing males using another  
471 trait [135; see also 142]. If males plastically adjust their investment into sexual traits that are  
472 still detectable by females [143] this could increase (or decrease) the variation in  
473 attractiveness among males depending on the ease with which females can discriminate

474 among males for different trait-environment combinations. In general, although many studies  
475 have documented that plastic responses affect which males mate or sire offspring, far fewer  
476 studies have quantified how this affects the net strength of sexual selection on different male  
477 traits.

478

### 479 *Plasticity and $r_G$*

480

481 To recap,  $r_G$  depends on  $V_A$  in male success under sexual competition,  $V_A$  in female LRS, and  
482 their covariation. We have already discussed how condition-dependence might affect  $V_A$  in  
483 male success via the heritability ( $V_A/V_P$ ) of male success. However, we glossed over the  
484 possibility that the proportion of  $V_A$  in male success attributable to condition changes across  
485 environments. This will affect the covariation between male success and female LRS. For  
486 example, if most  $V_A$  in male success is due to sexually antagonistic genes then  $r_G$  will be  
487 negative. A major consideration is therefore how male plasticity, other than that due to  
488 condition-dependence, affects the proportion of  $V_A$  in sexually selected traits attributable to  
489 sexually antagonistic genes. To our knowledge, few empirical or theoretical studies have  
490 explored this question. For example, does plastic expression by males of sexually selected  
491 traits in response to changes in social cues, such as lower population density in a novel  
492 environment, decrease the likelihood that male sexual traits are associated with genes that  
493 elevate female LRS?

494

### 495 **6. Direct effects of males on female reproductive output**

496 Males with greater expression of certain sexually selected traits can either elevate or depress  
497 the LRS of their mates (via  $r_P$ ) (§2a,b). For this to affect mean female LRS there must be  
498 sexual selection so that some males have higher mating success than others. More generally,

499 sexual competition among males can affect female LRS irrespective of which males end up  
500 mating (§2c). Any effect of male plasticity on mean female LRS therefore depends on how it  
501 affects the strength of sexual selection and which male traits increase males' success (i.e. are  
502 they those that increase or decrease female LRS?). We have already discussed the strength of  
503 selection in §5 so we now focus on plastic changes in selected male traits.

504

505 First, it seems self-evident that the mixture of plastic responses by males to social cues, the  
506 signalling environment and the total resources they acquire and assimilate (i.e. condition) due  
507 to being in a different environment makes it almost impossible to predict how resources will  
508 be allocated to different sexually and naturally selected traits. Less obvious, however, is the  
509 fact that it is still difficult to make predictions even if we only consider adaptive allocation of  
510 resources to different condition-dependent traits [95]. The adaptive response to an increase in  
511 condition driven by greater resource acquisition is to allocate these additional resources to the  
512 trait with the greatest marginal fitness gains. (In a novel environment, where fewer resources  
513 are available, we can treat this as a question of reduced investment into the trait where there  
514 will be the smallest marginal decrease in fitness.) This suggests that additional resources will  
515 be allocated exclusively to a single trait with the highest gain, such that only a single trait  
516 exhibits positive condition-dependence. There are, however, general reasons to believe that  
517 marginal fitness gains will not consistently differ among traits as a male's condition changes.  
518 First, investment into a trait often yields diminishing fitness gains. For example, whenever a  
519 trait increases the probability of a particular outcome, such as detection by potential mates, it  
520 cannot be increased beyond its maximum value of 1. Second, the marginal fitness gains from  
521 different traits are rarely independent. Fitness gains depend on the current values of other  
522 traits, and traits tend to function most efficiently if they are 'balanced' so that an individual  
523 operates as an integrated unit. For example, a longer tail ornament might be favoured by

524 female choice, but it will eventually become so long that investment into larger wings to  
525 maintain the ability to fly is likely to be more advantageous than a further increase in tail size.  
526 This should lead to plastic responses with increased expression of multiple traits in  
527 environments where males have access to more resources. Third, some traits might become  
528 more efficient (hence have greater fitness gains) when expressed at a higher absolute level  
529 [e.g. 144]. If so, greater condition could induce a shift in allocation that manifests as an  
530 increase in the focal trait, alongside a *decrease* in other (fitness-enhancing) traits [95]. This is  
531 one reason why both acquisition and allocation are themselves sometimes described as  
532 condition-dependent [e.g. 145].

533

534 Clearly, the sheer number of possible plastic responses by males to a change in condition that  
535 arise from being in a novel environment, make general predictions about plasticity in specific  
536 sexually selected traits problematic. There is no guarantee that greater condition leads to  
537 equal increases in all condition-dependent sexually (or naturally) selected traits. Broadly  
538 speaking, optimal condition-dependent allocation depends on the shape of the multivariate  
539 function that links traits to fitness. This function depends on species-specific details, such as  
540 morphological integration, the ecological context and, in the case of sexually selected traits,  
541 how the intensity and type of sexual selection (e.g. mating versus sperm competition) change  
542 with the environmental availability of resources that affect male and female condition.  
543 Consequently, when sexually selected traits vary in their effects on female LRS (e.g. a  
544 reduction in male song rate is unlikely to damage a female, while investment into seminal  
545 toxins is likely to induce female mortality), it is hard to determine whether condition-  
546 dependent plasticity will elevate or lower female LRS when males are in a novel (usually  
547 more stressful) environment.

548

549 When there are social cues about the level of mating or sperm competition there is often a  
550 clear theoretical prediction about how male investment will change for specific traits; and  
551 empirical studies typically report plastic responses in the predicted direction (i.e. greater  
552 investment in ejaculates as sperm competition increases) [review: 111]. However, as noted  
553 for condition-dependence, it is a challenge to predict the adaptive response when sexual  
554 selection acts on multiple traits. Specifically, the social setting could cause the marginal  
555 benefits of investment into different traits to change because of shifts in the relative  
556 importance of different sexual selection processes (e.g. courtship versus sperm competition).  
557 Even when models make predictions about optimal investment into testes versus  
558 weapons/ornaments in different social contexts [e.g. 94], they are hard to test because: (a)  
559 there are simplifying assumptions about the constancy of natural selection which do not apply  
560 if the social setting affects naturally selected traits; (b) most models predict evolution due to  
561 changes in gene frequencies, rather than the optimal plastic response, but the two outcomes  
562 are not necessarily in agreement (§8); (c) there is within-population variation in condition.  
563 All these factors makes it harder to predict the optimal plastic response for each individual  
564 [for a similar problem see 95].

565

566 Given no clear prediction about how males will allocate resources to different traits  
567 depending on their condition, determining the allocation patterns that are likely to arise in  
568 nature is chiefly an empirical matter. Even then, the relative amount of variation in  
569 acquisition versus allocation among individuals affects the observed population level  
570 correlations between traits [146; review: 145]. The two main areas with relevant data are: (a)  
571 whether condition-dependent male sexual signals are honest indicators of parental care, and  
572 (b) whether males with greater investment into sexually selected traits (preferred males, or

573 males that win fights for access to females), benefit or harm their mating partners compared  
574 to the average male.

575

576 (a) A ‘good parent’ model suggests that condition-dependent sexual traits honestly signal  
577 parental care, while ‘differential allocation’ models predict that sexual selection on males  
578 lowers parental care due to the resource trade-offs that males face [147-149]. This is why the  
579 relationship between condition-dependent male sexual signal and paternal care is unclear, and  
580 both outcomes seem possible [150]. However, the fact that female mating preferences might  
581 evolve in response to the direction of the relationship would appear to favour males being  
582 ‘good parents’, which could even lead to the evolution of male-only care [151]. But the  
583 enduring challenge is to explain why attractive males provide more care when mating  
584 precedes caring. In general, there must be inherent constraints on preferred males, perhaps  
585 due to the social setting (e.g. strict monogamy [149], or because early mate desertion by  
586 females increases the value of male care [152]), such that males gain more by providing the  
587 ‘advertised’ care than redirecting resources to pursue additional mating opportunities [see  
588 also 153]. The extent to which such constraints are associated with plastic male responses to  
589 condition due to environmental variation is an open question, but it is one way in which  
590 plasticity could facilitate the process of sexual selection increasing mean female LRS. In  
591 general, there is high variation among species in the link between male sexual trait expression  
592 and how it effects female LRS through parental care, fertilization success, or other factors  
593 that influence female fecundity (e.g. nuptial gifts) [55].

594

595 (b) It seems unlikely that females would prefer males that lower their LRS, but this occurs in  
596 some species, and presumably reflects an on-going ‘arms race’ between seduction and  
597 resistance that males are currently ‘winning’ [e.g. 50,51,154]. Mating with males who are

598 more sexually competitive can still increase a female's fitness even if it lowers her LRS if the  
599 costs of mating resistance are higher than accepting such males as mates. However, selection  
600 on females could lead to the evolution of the ability of females to reduce mating costs [155].  
601 The net effect is that sexual selection on males can lower mean female LRS. But, to what  
602 extent does male plasticity influence this process? First, condition-dependent expression of  
603 damaging male traits might magnify the harmful effects of mating with more sexually  
604 competitive males. Intriguingly, however, we know of no systematic review that determines  
605 the extent to which, for example, experimental manipulation of male condition is associated  
606 with increased expression of specific male traits that appear to harm females such as seminal  
607 toxins and genital structures [but see 156]. There is, however, evidence that social cues of the  
608 intensity of sperm competition lead to plastic responses in ejaculates (e.g. protein content and  
609 sperm count) that lower female LRS [122,157]. In addition, recent studies suggest that greater  
610 relatedness between competing males can result in phenotypic responses that reduce the  
611 extent to which males lower female LRS when competing for fertilizations [e.g. 158,159].

612

## 613 **7. Plasticity and females**

614 We have emphasized sexual selection on males but, of course, sexual selection also acts on  
615 females (e.g. female-female competition for breeding opportunities and male mate choice)  
616 [reviews: 30,160,161]. What effect do sexually selected female traits have on mean female  
617 LRS? Clearly, mean female LRS must decline if there is any fitness trade-off with naturally  
618 selected traits [162]. If females simply used a lottery rather than expend resources on  
619 competition to determine contested breeding opportunities, then the 'winning' female could  
620 invest more in reproduction. Of course, the same is true for males, but a key difference is that  
621 the mean LRS of breeders is likely to be more strongly affected by which females, rather than  
622 males, breed. This claim is based on the assumption that there is greater variation in female



623 fecundity and parental investment than in direct male effects on female LRS (§2b). A more  
624 interesting question is: to what extent does plasticity in sexually selected female traits  
625 increase the realised fecundity of breeders when breeding sites and/or male mates are a  
626 limited resource? If female investment in sexually selected traits is condition-dependent, but  
627 the proportion of resources invested is smaller for females in better condition (so that they  
628 remain more fecund), then plasticity might increase the mean LRS relative to that observed if  
629 females stochastically acquired breeding opportunities. To our knowledge, the circumstances  
630 where condition-dependence of female sexually selected traits elevates mean female LRS  
631 have not been formally modelled. We refer the reader to [162] for an extensive review of  
632 female ornament evolution.

633

634 Female plasticity is mainly studied by asking how it affects male-imposed costs, or how it  
635 allows a female to choose males that increase her LRS or the fitness of her offspring. We  
636 consider both. First, recent models examine in detail how plasticity affects sexually  
637 antagonistic selection [163,164]. Specifically, they ask how it affects the conflict load (fitness  
638 reduction compared to a hypothetical best-case scenario) of individuals involved in pairwise  
639 interactions, when each party controls an antagonistic trait that decreases the other party's  
640 fitness. The focus is on a situation where plasticity is unilateral, i.e. only one party shows a  
641 plastic response, while the other's strategy evolves due to differential success of genotypes.  
642 An illustrative case in which females are the plastic party is post-copulatory sexual conflict,  
643 where males commit to a strategy by transferring seminal fluid proteins (SFPs) that females  
644 then respond to plastically. The general finding is that plasticity, compared to neither party  
645 showing plasticity, always reduces the conflict load of the non-plastic party, but that of the  
646 other party can either increase or decrease [163,164]. The intuitive reason is as follows. There  
647 are two directions in which an individual of party *P* (for 'plastic') might adjust its

648 antagonistic trait  $p$  when faced with a mutant of party  $N$  (for ‘non-plastic’) with a slightly  
649 deviant antagonistic trait  $n$ . If  $p$  is adjusted in the same direction as the change in  $n$  (i.e. less  
650 antagonistic mutants elicit a less antagonistic response), then plasticity selects for lower  
651 antagonism in  $N$ . By contrast, if  $p$  is adjusted such that more antagonistic mutants elicit a less  
652 antagonistic response, then plasticity selects for greater antagonism in  $N$ . Thus, depending on  
653 the direction of the plastic response, plasticity either selects for more or less antagonism in  $N$ ,  
654 either increasing or reducing  $P$ ’s conflict load. In contrast,  $N$ ’s conflict load always decreases  
655 because  $N$  always evolves in the direction that elicits a less antagonistic response. This is an  
656 intriguing result, but its applicability to post-copulation sexual conflict probably depends on  
657 biological details. For example, if SFPs elevate the oviposition rate, but females can restore a  
658 nearly optimal rate with a plastic response, the evolution of more SFPs need not increase the  
659 conflict load for females. Instead, regardless of the absolute amount of SFPs transferred, the  
660 females’ conflict load might reflect only the extent to which they are actually manipulated.  
661 Similarly, regardless of the absolute magnitude of a ‘female resistance trait’, a male’s conflict  
662 load might reflect only the extent to which his mate’s oviposition rate deviates from his  
663 optimum. There is no compelling reason why this deviation will necessarily be smaller when  
664 females exhibit a plastic rather than an evolved response.

665

666 Second, many studies have investigated plasticity in female mate choice. Empirical studies  
667 have shown that choice is plastically adjusted to external factors, such as the energetic costs  
668 of mate sampling, and that shifts in the threshold for acceptable mates occur based on the  
669 type and rate at which prospective males are encountered [165]. There is also good empirical  
670 evidence that female mate choice is often condition-dependent [166]. It is reasonable to  
671 assume initially that these are mainly cases of adaptive plasticity because the inherent costs of  
672 mate choice suggest that selection favours random mating if choosiness provides no benefits

673 [49]. The genetic benefits of choosing certain males as mates are small or absent in many  
674 species [167], so adaptive mate choice implies that plasticity is likely to elevate female LRS.  
675 It should be noted, however, that while plasticity might increase female LRS in the short-  
676 term, it could favour the evolution of male traits that lower female LRS. An obvious example  
677 is that greater mean female choosiness due to plasticity selects more strongly for coercive  
678 male traits that tend to lower females' fecundity or longevity [62].

679

680 If natural selection acts similarly in both sexes there is a scenario in which condition-  
681 dependent female choice can elevate mean female LRS. The opening premise is that local  
682 adaptation is reduced when natural selection differs among populations and there is gene flow  
683 (migration). The rate of local adaptation is increased if females prefer locally adapted males,  
684 thereby reducing gene flow. In general, female mating preferences lead to local adaptation if  
685 they favour males in good condition (i.e. locally adapted) [but see 13 for complexities]. This  
686 general idea was modelled by [168] who developed a simple model with two patches that  
687 differ ecologically and two evolving traits: an ecological trait and a female mating preference.  
688 The strength of the preference for males in good condition was contingent on the female's  
689 ecological fit to the local patch (i.e. her condition). In this case, condition-dependent female  
690 preferences facilitate local adaptation: the costs of choice tend to slow the spread of a mating  
691 preference, but with condition dependence these costs are disproportionately born by poorly  
692 adapted females (who are in worse condition) thereby lowering their fitness relative to that of  
693 better adapted females.

694

## 695 **8. Do adaptive plastic responses mirror the direction of evolution?**

696 It is tempting to assume that adaptive plasticity will produce a phenotypic shift in the same  
697 direction as selection on genotypes for fixed traits. This assumption is not universally

698 justified. For example, Kahn et al. [169] modelled sex allocation decisions where mothers can  
699 re-allocate parental resources to produce more offspring when some die during the period of  
700 parental investment. They examined the effect of environmental stress that increases the  
701 mortality of sons during the period of parental investment. Although the adaptive plastic  
702 response of mothers is to produce *fewer* sons when only some mothers experience this stress,  
703 the population as a whole will evolve to produce *more* sons when the stress applies globally.  
704 This pattern arises because a locally-favoured trait (i.e. producing daughters) faces negative  
705 frequency-dependent selection at the population level, so it is not universally advantageous.  
706 Opposing directions of adaptive and evolved responses could occur in many other frequency-  
707 dependent selection scenarios.

708

709 More generally, game theory often predicts the coexistence of alternative phenotypes under  
710 negative frequency-dependent selection in a mixed Evolutionarily Stable Strategy (ESS)  
711 [170]. A mixed ESS can manifest either as a genetic polymorphism or probabilistic  
712 expression of phenotypes (at the same frequencies as fixed phenotypes). However, if  
713 heterogeneity in local factors makes one phenotype slightly advantageous, then selection  
714 might favour a plastic response to produce the locally favoured phenotype. For example, in  
715 some spiders a mixed ESS is predicted whereby males are either monogynous (mate with one  
716 female only) or bigynous (mate with two females) [171]. If the mortality risk of mate-  
717 searching varies among males, then males with a below-average risk should plastically  
718 exhibit bigyny [172]. But, depending on the adult sex ratio, greater mortality costs of mate  
719 searching at the population level can either increase or decrease the frequency of bigyny  
720 [171]. Whether or not adaptive plastic responses match the direction of evolution of fixed  
721 differences in response to the same environmental cues depends on details that do not readily  
722 permit generalisations. However, mismatch hinges on negative frequency-dependent

723 selection, and many adaptations are frequency-independent (e.g. temperature tolerance). If  
724 selection on a trait is frequency-independent, we suggest that it will usually be true that,  
725 following an environmental change, adaptive phenotypic plasticity and selection on mean  
726 trait values will shape phenotypes to evolve in the same direction.

727

## 728 **9. Summary**

729

730 Whether sexual selection hastens female adaptation to environmental change, and thereby  
731 reduces the likelihood of population extinction, is unresolved [5,11,13]. The extent to which  
732 male phenotypic plasticity further enhances or diminishes the effect of sexual selection is  
733 even harder to discern. We focussed on female LRS rather than, as is standard in sexual  
734 selection models, mean offspring fitness. We mainly concentrated on a few ideas. First,  
735 sexual selection changes the likelihood of population extinction if it affects which males mate  
736 *and* this influences how many females breed and their mean LRS. Second, although a range  
737 of environmental cues induce plastic responses in sexually selected male traits, the condition-  
738 dependence of these traits is the factor most likely to affect female LRS in a changing  
739 environment. This is because, under such circumstances, sexually competitive males are more  
740 likely to transfer genes that elevate female LRS than to have sexually antagonistic effects.  
741 Third, condition-dependence is important when the environment changes because it can alter  
742 the strength of sexual selection, affect who mates, and change the allocation of resources to  
743 different sexually selected traits that vary in the extent to which they benefit or harm females.  
744  
745 We conclude that there are no general rules determining whether plasticity of sexually  
746 selected traits will reduce or elevate the risk of population extinction. This unsatisfying, but  
747 almost inevitable, conclusion concurs with inferences drawn about the effects of phenotypic

748 plasticity on eco-evolutionary dynamics [173]. There is, however, a glimmer of hope. Recent  
749 theoretical models of sexual conflict over mating [163,164], offspring sex ratio adjustment  
750 based on sire attractiveness [60,174], and whether plastic maternal effects are more likely  
751 than plastic responses by offspring to generate adaptive outcomes [175] all show that there is  
752 the potential to make predictions about the extent to which different forms of phenotypic  
753 plasticity in sexually selected and allied traits facilitate adaptive evolution. The challenge  
754 now is to produce models that explicitly incorporate phenotypic plasticity, in order to ask  
755 questions about the role of sexual selection in facilitating population persistence in the face of  
756 rapid environmental change [see 176].

757

758 Data accessibility: This article has no additional data.

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765

## 766 **References**

767

768 1. Servedio MR, Van Doorn GS, Kopp M, Frame AM, Nosil P. 2011 Magic traits in  
769 speciation: ‘magic’ but not rare. *Trends Ecol. Evol.* **26**, 389-397.

770

771 2. Mérot C, Frérot R, Leppik E, Joron M. 2015 Beyond magic traits: multimodal mating cues  
772 in *Heliconius* butterflies. *Evolution* **69**, 2891-2904.

773

774 3. Candolin U, Heuschele J. 2008 Is sexual selection beneficial during adaptation to  
775 environmental change? *Trends Ecol. Evol.* **23**, 446–452.

776

777 4. Holman L, Kokko H. 2014 Local adaptation and the evolution of female choice. *In* J Hunt  
778 & D Hosken (eds) *Genotype-by-Environment Interactions and Sexual Selection*. Wiley-  
779 Blackwell. pp 41-62.

780

781 5. Martínez-Ruiz C, Knell RJ. 2017 Sexual selection can both increase and decrease  
782 extinction probability: reconciling demographic and evolutionary factors. *J. Anim. Ecol.*  
783 **86**,117-127.

784

785 6. Servedio MR, Boughman JW. 2017 The role of sexual selection in local adaptation and  
786 speciation. *Annu. Rev. Ecol. Evol. Syst.* **48**, 85–109.

787

788 7. Allen SL, McGuigan K, Connallon T, Blows MW, Chenoweth SF. 2017 Sexual selection  
789 on spontaneous genetic mutations strengthens the between-sex genetic correlation for fitness.  
790 *Evolution* **71**, 2398-2409.

791

792 8. Hendry AP, Schoen DJ, Wolak ME, Reid JM. 2018 The contemporary evolution of fitness.  
793 *Annu. Rev. Ecol. Evol. Syst.* **49**, 457-476.

794

795 9. Lande R. 1993 Risks of population extinction from demographic and environmental  
796 stochasticity and random catastrophes. *Am. Nat.* **142**, 911-927.

797

- 798 10. Snell-Rood EC, Kobiela ME, Sikkink KL, Shepherd AM. 2018 Mechanisms of plastic  
799 rescue in novel environments. *Annu. Rev. Ecol. Evol. Syst.* **49**, 331-354.  
800
- 801 11. Holman L, Kokko H. 2013 The consequences of polyandry for population viability,  
802 extinction risk and conservation. *Phil. Trans. Roy. Soc. B.* **368**, 20120053.  
803
- 804 12. Wright S. 1969 *Evolution and Genetics of Populations. Vol. 2. The Theory of Gene*  
805 *Frequencies*. The University of Chicago Press, Chicago.  
806
- 807 13. Li X-Y, Holman L. 2018 Evolution of female choice under intralocus sexual conflict and  
808 genotype-by-environment interactions. *Phil. Trans. Roy. Soc. B.* **373**, 20170425.  
809
- 810 14. Cornwallis CK, Uller T. 2010 Towards an evolutionary ecology of sexual traits. *Trends*  
811 *Ecol. Evol.* **25**, 145-152.  
812
- 813 15. Rosenthal GG. 2018 Evaluation and hedonic value in mate choice. *Curr. Zool.* **64**, 485-  
814 492.  
815
- 816 16. Kokko H, Rankin DJ. 2006 Lonely hearts or sex in the city? Density-dependent effects in  
817 mating systems. *Phil. Trans. Roy. Soc. B.* **28**, 319-334.  
818
- 819 17. Lüpold S, Tomkins JL, Simmons LW, Fitzpatrick JL. 2014 Female monopolisation  
820 mediates the relationship between pre- and postcopulatory sexual traits. *Nat. Comm.* **5**, 3184.  
821



- 822 18. Henshaw J, Kokko H, Jennions MD. 2015 Direct reciprocity stabilise simultaneous  
823 hermaphroditism at high mating rates: a model of sex allocation with egg trading and  
824 hermaphrodites. *Evolution* **69**, 2129-2139.
- 825
- 826 19. Queller DC. 1997 Why do females care more than males? *Proc. Roy. Soc. B.* **264**, 1555-  
827 1557.
- 828
- 829 20. Kokko H, Jennions MD. 2008 Parental investment, sexual selection and sex ratios. *J.*  
830 *Evol. Biol.* **21**, 919-948.
- 831
- 832 21. Fromhage L, Jennions MD. 2016 Coevolution of parental investment and sexually  
833 selected traits drives sex role divergence. *Nat. Comm.* **7**, 12517.
- 834
- 835 22. Andersson M. 1994. *Sexual Selection*. Princeton University Press, NJ pp 599.
- 836
- 837 23. Clutton-Brock T. 2007 Sexual selection in males and females. *Science* **318**, 1882-1885.
- 838
- 839 24. Dale J, Dey CJ, Delhey K, Kempenaers B, Valcu M. 2015. The effects of life history and  
840 sexual selection on male and female plumage colouration. *Nature* **527**, 367-370.
- 841
- 842 25. McCullough EL, Miller CW, Emlen DJ. 2016 Why sexually selected weapons are not  
843 ornaments. *Trends Ecol. Evol.* **31**, 742-751.
- 844
- 845 26. Janicke T, Häderer IK, Lajeunesse MJ, Anthes N. 2016 Darwinian sex roles confirmed  
846 across the animal kingdom. *Sci. Adv.* **2**, e1500983.

847

848 27. Henshaw JM, Kahn AT, Fritzsche K. 2016 A rigorous comparison of sexual selection  
849 indices via simulations of diverse mating systems. *Proc. Nat. Acad. Sci.* **113**, E300-E308.

850

851 28. Henshaw JM, Jennions MD, Kruuk LEB. 2018 How to quantify (the response to) sexual  
852 selection on traits. *Evolution* doi 10.1111/evo.13554.

853

854 29. Stockley P, Bro-Jørgensen J. 2011 Female competition and its evolutionary consequences  
855 in mammals. *Biol. Rev.* **86**, 341-366.

856

857 30. Hare RM, Simmons LW. 2019 Sexual selection and its evolutionary consequences in  
858 female animals. *Biol. Rev.* (in press)

859

860 31. Gienapp P, Brommer JE. 2014 Evolutionary dynamics in response to climate change. *In*  
861 A Charmantier, D Garant & LEB Kruuk (eds) *Quantitative Genetics in the Wild*. Oxford  
862 University Press, Oxford, UK. pp 254-274.

863

864 32. Rankin DJ, Kokko H. 2007 Do males matter? The role of males in population dynamics.  
865 *Oikos* **116**, 335-348.

866

867 33. Radwan J. 2008 Maintenance of genetic variation in sexual ornaments: a review of the  
868 mechanisms. *Genetica* **134**, 113-127.

869

870 34. Berger D, Grieshop K, Lind MI, Goenaga J, Maklakov AA, Arnqvist G. 2014 Intralocus  
871 sexual conflict and environmental stress. *Evolution* **68**, 2184-2196.

872

873 35. Connallon T, Jakubowski E. 2009 Association between sex ratio distortion and sexually  
874 antagonistic fitness consequences of female choice. *Evolution* **63**, 2179-2183.

875

876 36. Connallon T, Clark AG. 2014 Evolutionary inevitability of sexual antagonism. *Proc. R*  
877 *Soc. B.* **281**, 20132123.

878

879 37. Chippindale AK, Gibson JR, Rice WR. 2001 Negative genetic correlation for adult fitness  
880 between sexes reveals ontogenetic conflict in *Drosophila*. *Proc. Natl Acad. Sc. USA.* **98**,  
881 1671–1675.

882

883 38. Pischedda A, Chippindale AK. 2006 Intralocus sexual conflict diminishes the benefits of  
884 sexual selection. *PLoS Biol.* **4**, e356.

885

886 39. Brommer JE, Kirkpatrick M, Qvarnström A, Gustafsson L. 2007 The intersexual genetic  
887 correlation for lifetime fitness in the wild and its implications for sexual selection. *PLoS*  
888 *One* **2**, e744.

889

890 40. Foerster K, Coulson T, Sheldon BC, Pemberton JM, Clutton-Brock TH, Kruuk  
891 LEB. 2007 Sexually antagonistic genetic variation for fitness in red deer. *Nature* **447**, 1107–  
892 1110.

893

894 41. Mokkonen M, Kokko H, Koskela E, Lehtonen J, Mappes T, Martiskainen H, Mills  
895 SC. 2011 Negative frequency-dependent selection of sexually antagonistic alleles in *Myodes*  
896 *glareolus*. *Science* **334**, 972–974.

897

898 42. Parsch J, Ellegren H. 2013 The evolutionary causes and consequences of sex-biased gene  
899 expression. *Nat. Rev. Genet.* **14**, 83-87.

900

901 43. Allen SL, Bonduriansky R, Chenoweth SF. 2018 Genetic constraints on  
902 microevolutionary divergence of sex-biased gene expression. *Phil. Trans. R. Soc. B.* **373**,  
903 20170427.

904

905 44. Connallon T, Debarre F, Li X-Y. 2018 Linking local adaptation with the evolution of sex  
906 differences. *Phil. Trans. Roy. Soc. B.* **373**, 20170414.

907

908 45. Connallon T. 2015 The geography of sex-specific selection, local adaptation, and sexual  
909 dimorphism. *Evolution* **69**, 2333-2344.

910

911 46. Connallon T, Hall MD. 2016 Genetic correlations and sex-specific adaptation in changing  
912 environments. *Evolution* **70**, 2186-2198.

913

914 47. Kokko H, Jennions MD, Brooks R. 2006 Unifying and testing models of sexual selection.  
915 *Ann. Rev. Ecol. Evol. Syst.* **37**, 43-66.

916

917 48. Fawcett TW, Kuijper B, Pen I, Weissing FJ. 2007 Should attractive males have more  
918 sons? *Behav. Ecol.* **18**, 71-80.

919

920 49. Kuijper B, Pen I, Weissing FJ. 2012 A guide to sexual selection theory. *Annu. Rev. Ecol.*  
921 *Evol. Syst.* **43**, 287-311.

922  
923  
924  
925  
926  
927  
928  
929  
930  
931  
932  
933  
934  
935  
936  
937  
938  
939  
940  
941  
942  
943  
944  
945  
946

50. Pitnick S, Garcia-González F. 2002 Harm to females increases with male body size in *Drosophila melanogaster*. *Proc. Roy. Soc. B.* **269**, 1821-1828.

51. Bilde T, Foged A, Schilling N, Arnqvist G. 2009 Postmating sexual selection favors males that sire offspring with low fitness. *Science* **324**, 1705–1706.

52. Iglesias-Carrasco M, Jennions MD, Zajitschek S, Head ML. 2018 Are females in good condition better able to cope with costly males? *Behav. Ecol.* **29**, 876-884.

53. Kokko H, Ranta E, Ruxton G, Lundberg P. 2002 Sexually transmitted disease and the evolution of mating systems. *Evolution* **56**, 1091-1100.

54. Ashby B, Gupta S. 2013 Sexually transmitted infections in polygamous mating systems. *Phil. Trans. Roy. Soc. B.* **368**, 20120048.

55. Møller A, Jennions M. 2001 How important are direct fitness benefits of sexual selection? *Naturwissenschaften* **88**, 401-415.

56. Kelly NB, Alonzo S. 2009 Will male advertisement be a reliable indicator of paternal care, if offspring survival depends on male care? *Proc. Roy. Soc. B.* **276**, 3175-3183.

57. Sibly RM, Witt CC, Wright NA, Venditti C, Jetz W, Brown JH. 2012 Energetics, lifestyle, and reproduction in birds. *Proc. Nat. Acad. Sci. USA* **109**, 10937-10941.

947 58. Bussière LF. 2002 A model of the interaction between ‘good genes’ and direct benefits I  
948 courtship-feeding animals: when do males of high genetic quality invest less? *Phil. Trans.*  
949 *Roy. Soc. B.* **357**, 309-317.

950

951 59. Bussière LF, Abdul Basit H, Gwynne DT. 2005 Preferred males are not always good  
952 providers: female choice and male investment in tree crickets. *Behav. Ecol.* **16**, 223-231.

953

954 60. Fawcett TW, Kuijper B, Weissing FJ, Pen I. 2011 Sex-ratio control erodes sexual  
955 selection, revealing evolutionary feedback from adaptive plasticity. *Proc. Nat. Acad. Sci.*  
956 *USA.* **108**, 15925-15930.

957

958 61. Booksmythe I, Mautz B, Davis J, Nakagawa S, Jennions MD. 2017 Facultative  
959 adjustment of the offspring sex ratio and male attractiveness: a systematic review and meta-  
960 analysis. *Biol. Rev.* **92**, 108-134.

961

962 62. Arnqvist G, Rowe L. 2005 *Sexual conflict*. Princeton, NJ: Princeton University Press.

963

964 63. Wedell N, Gage MJG, Parker GA. 2002 Sperm competition, male prudence and sperm-  
965 limited females. *Trends Ecol. Evol.* **17**, 313-320.

966

967 64. Bro-Jørgensen J. 2007 Reversed sexual conflict in a promiscuous antelope. *Curr. Biol.*  
968 **17**, 2157-2161.

969

970 65. Morrow EH, Arnqvist G. 2003 Costly traumatic insemination and a female counter-  
971 adaptation in bed bugs. *Proc. R. Soc. Lond. B.* **270**, 2377-2381.

972  
973  
974  
975  
976  
977  
978  
979  
980  
981  
982  
983  
984  
985  
986  
987  
988  
989  
990  
991  
992  
993  
994  
995  
996

66. Le Galliard J-F, Cote J, Fitze PS. 2008 Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. *Ecology* **89**, 56-64.

67. Gay L, Eady PE, Vasudev R, Hosken DJ, Tregenza T. 2009 Costly sexual harassment in a beetle. *Phys Ent.* **34**, 86-92.

68. Rice W, Gavrilets S. 2014 *The Genetics and Biology of Sexual Conflict*. Cold Spring Harbor Perspectives in Biology, Cold Spring Harbor Press. pp432

69. Perry JC, Rowe L. 2018 Sexual conflict in its ecological setting. *Phil. Trans. Roy. Soc. B.* **373**, 20170418.

70. Long TAF, Agrawal AF, Rowe L. 2012 The effect of sexual selection on offspring fitness depends on the nature of genetic variation. *Curr. Biol.* **22**, 204–208.

71. Martinossi-Allibert I, Rueffler C, Arnqvist G, Berger D. 2018 The efficacy of sexual selection under environmental change. *bioRxiv* doi:10.1101/283457.

72. Skwierzynska AM, Radwan J, Piesnar-Bielak A. 2018 Male-limited secondary sexual trait interacts with environment in determining female fitness. *Evolution* doi 10.1111/evo.13551.

73. Kraaijeveld K, Kraaijeveld-Smit FJ, Maan ME. 2011 Sexual selection and speciation: the comparative evidence revisited. *Biol. Rev.* **86**, 367-377.

- 997 74. Janicke T, Ritchie MG, Morrow EH, Marie-Orleach L. 2018 Sexual selection predicts  
998 species richness across the animal kingdom. *Proc. Roy. Soc. B.* **285**, 20180173.  
999
- 1000 75. Huang H, Rabosky DL. 2014 Sexual selection and diversification: re-examining the  
1001 correlation between dichromatism and speciation rate in birds. *Am. Nat.* **184**, E101-114.  
1002
- 1003 76. Servedio MR, Bürger R. 2014 The counterintuitive role of sexual selection in species  
1004 maintenance and speciation. *Proc. Nat. Acad. Sci. USA* **111**, 8113-8118.  
1005
- 1006 77. Martins MJE, Puckett TM, Lockwood R, Swaddle JP, Hunt G. 2018 High male sexual  
1007 investment as a driver of extinction in fossil ostracods. *Nature* **556**, 366-369.  
1008
- 1009 78. Edward DA, Fricke C, Chapman T. 2010 Adaptations to sexual selection and sexual  
1010 conflict: insights from experimental evolution and artificial selection. *Phil. Trans. Roy. Soc.*  
1011 *B.* **365**, 2541-2548.  
1012
- 1013 79. Firman RC, Simmons LW. 2011 Experimental evolution of sperm quality via  
1014 postcopulatory sexual selection in house mice. *Evolution* **64**, 1245-1256.  
1015
- 1016 80. Power DJ, Holman L. 2014 Polyandrous females found fitter populations. *J. Evol. Biol.*  
1017 **27**, 1948-1955.  
1018
- 1019 81. Alombro M, Simmons LW. 2014 Sexual selection can remove an experimentally induced  
1020 mutation load. *Evolution* **68**, 295-300.  
1021



- 1022 82. Hollis B, Houle D. 2011 Populations with elevated mutation load do not benefit from the  
1023 operation of sexual selection. *J. Evol. Biol.* **24**, 1918-1926.  
1024
- 1025 83. Innocenti P, Morrow EH, Dowling D. 2011 Experimental evidence supports a sex-  
1026 specific selective sieve in mitochondrial genome evolution. *Science* **332**, 845-848.  
1027
- 1028 84. Fritzsche K, Booksmythe I, Arnqvist G. 2016 Sex ratio bias leads to the evolution of sex  
1029 role reversal in honey locust beetles. *Curr. Biol.* **26**, 2522-2526.  
1030
- 1031 85. Jarzebowski M, Radwan, J. 2010 Sexual selection counteracts extinction of small  
1032 populations of the bulb mites. *Evolution* **64**, 1283-1289.  
1033
- 1034 86. Plesnar-Bielak A., Skrzynecka AM, Prokop ZM, Radwan J. 2012 Mating system affects  
1035 population performance and extinction risk under environmental challenge. *Proc. Roy. Soc.*  
1036 *B.* **279**, 4661–4667.  
1037
- 1038 87. Price TAR, Hurst GDD, Wedell N. 2010 Polyandry prevents extinction. *Curr. Biol.* **20**,  
1039 471-475.  
1040
- 1041 88. Lumley AJ, Michalczyk L, Kitson JJN, Spurgin LG, Morrison CA, Godwin MED, Martin  
1042 OY, Emerson BC, Chapman T, Gage MJG. 2015 Sexual selection protects against extinction.  
1043 *Nature* **522**, 470-473.  
1044
- 1045 89. DeWitt TJ, Sih A, Wilson DS. 1998 Costs and limits of phenotypic plasticity. *Trends*  
1046 *Ecol. Evol.* **13**, 77-81.

1047

1048 90. Auld JR, Agrawal AA, Relyea RA. 2010 Re-evaluating the costs and limits of adaptive  
1049 phenotypic plasticity. *Proc. R. Soc. B* **277**, 503-511.

1050

1051 91. Constantini D, Monaghan P, Metcalfe NB. 2014 Prior hormetic priming is costly under  
1052 environmental mismatch. *Biol. Lett.* **10**, 20131010.

1053

1054 92. Murren CJ, Auld JR, Callahan H, Ghalambor CK, Handelsman CA, Heskell MA,  
1055 Kingsolver JG, Maclean HJ, Masel J, Maughan H, Pfennig DW, Relyea RA, Seiter S, Snell-  
1056 Rood E, Steiner UK, Schlichting CD. 2015 Constraints on the evolution of phenotypic  
1057 plasticity: limits and costs of phenotype and plasticity. *Heredity* **115**, 293-301.

1058

1059 93. Rowe L, Houle D. 1996 The lek paradox and the capture of genetic variance by condition  
1060 dependent traits. *Proc R Soc Lond B.* **263**, 1415-1421.

1061

1062 94. Parker GA, Lessells CM, Simmons LW. 2013 Sperm competition games: A general  
1063 model for pre-copulatory male– male competition. *Evolution* **67**, 95–109.

1064

1065 95. Hooper AK, Lehtonen J, Schwanz LE, Bonduriansky R. 2018 Sexual competition and the  
1066 evolution of condition-dependent ageing. *Evol. Lett.* **2**, 37-48.

1067

1068 96. Tomkins JL, Radwan J, Kotiaho JS, Tregenza T. 2004 Genic capture and resolving the  
1069 lek paradox. *Trends Ecol. Evol.* **19**, 323-328.

1070

1071 97. Morehouse NI. 2014 Condition-dependent ornaments, life-histories, and the evolving  
1072 architecture of resource-use. *Integr. Comp. Biol.* **54**, 591-600.  
1073

1074 98. Cotton S, Fowler K, Pomiankowski A. 2004 Do sexual ornaments demonstrate  
1075 heightened condition-dependent expression as predicted by the handicap hypothesis? *Proc.*  
1076 *Roy. Soc. B.* **271**, 771-783.  
1077

1078 99. Delhey K, Szecsenyi B, Nakagawa S, Peters A. 2017 Conspicuous plumage colours are  
1079 highly variable. *Proc. R. Soc. B.* **284**, 20162593.  
1080

1081 100. Rohner PT, Teder T, Esperk T, Lüpold S, Blanckenhorn WU. 2018 The evolution of  
1082 male-biased sexual size dimorphism is associated with increased body size plasticity in  
1083 males. *Func. Ecol.* **32**, 581-591.  
1084

1085 101. Bonduriansky R. 2007 The evolution of condition-dependent sexual dimorphism. *Am.*  
1086 *Nat.* **169**, 9-19.  
1087

1088 102. Dmitriew C, Blanckenhorn WU. 2014 Condition dependence and the maintenance of  
1089 genetic variance in a sexually dimorphic black scavenger fly. *J. Evol. Biol.* **27**, 2408-2419.  
1090

1091 103. Ingleby FC, Hunt J, Hosken DJ. 2010 The role of genotype-by-environment interactions  
1092 in sexual selection. *J. Evol. Biol.* **23**, 2031-2045.  
1093

- 1094 104. Evans JP, Garcia-Gonzalez F. 2016 The total opportunity for sexual selection and the  
1095 integration of pre- and post-mating episodes of sexual selection in a complex world. *J. Evol.*  
1096 *Biol.* **29**, 2338-2361.
- 1097
- 1098 105. Whitlock MC. 2000 Fixation of new alleles and the extinction of small populations: drift  
1099 load, beneficial alleles, and sexual selection. *Evolution* **54**, 1855–1861.
- 1100
- 1101 106. Whitlock MC, Agrawal AF. 2009 Purging the genome with sexual selection: reducing  
1102 mutation load through selection on males. *Evolution* **63**, 569–82.
- 1103
- 1104 107. Chenoweth SF, Appleton NC, Allen SL, Rundle H. 2015 Genomic evidence that sexual  
1105 selection impedes adaptation to a novel environment. *Curr. Biol.* **25**, 1860-1866.
- 1106
- 1107 108. Martinossi-Allibert I, Savković U, Đorđević M, Arnqvist G, Stojković B, Berger D.  
1108 2018 The consequences of sexual selection in well-adapted and maladapted populations of  
1109 bean beetles. *Evolution* **72**, 518-530.
- 1110
- 1111 109. Perry JC, Rowe L. 2010 Condition-dependent ejaculate size and composition in a  
1112 ladybird beetle. *Proc. R. Soc. B.* **277**, 3639-3647.
- 1113
- 1114 110. Parker GA, Pizzari T. 2010 Sperm competition and ejaculate economics. *Biol. Rev.* **85**,  
1115 897–934.
- 1116
- 1117 111. Bretman A, Gage MJG, Chapman T. 2011 Quick-change artists: male plastic  
1118 behavioural responses to rivals. *Trends Ecol. Evol.* **26**, 467-473.

1119

1120 112. Weir LK, Grant JWA, Hutchings JA. 2011 The influence of operational sex ratio on the  
1121 intensity of competition for mates. *Am. Nat.* **177**, 167-176.

1122

1123 113. Kelly CD, Jennions MD. 2011 Sexual selection and sperm quantity: meta-analyses of  
1124 strategic ejaculation. *Biol. Rev.* **86**, 863-884.

1125

1126 114. Simmons LW, Lupold S, Fitzpatrick JL. 2017 Evolutionary trade-off between secondary  
1127 sexual traits and ejaculates. *Trends Ecol. Evol.* **32**, 964-976.

1128

1129 115. Bretman A, Westmancoat JD, Gage MJG, Chapman T. 2012 Individual plastic  
1130 responses by males to rivals reveal mismatches between behaviour and fitness outcomes.  
1131 *Proc. Roy. Soc. B.* **279**, 2868-2876.

1132

1133 116. Bretman A, Westmancoat JD, Gage MJG, Chapman T. 2013 Costs and benefits of  
1134 lifetime exposure to mating rivals in male *Drosophila melanogaster*. *Evolution* **67**, 2413-  
1135 2422.

1136

1137 117. Iglesias Carrasco M, Bilgin G, Jennions MD, Zajitschek S, Head ML. 2018 The fitness  
1138 cost to females of exposure to males does not depend on water availability in seed beetles.  
1139 *Anim. Behav.* **142**, 77-84.

1140

1141 118. Friberg U. 2006 Male perception of female mating status: its effect on copulation  
1142 duration, sperm defence and female fitness. *Anim. Behav.* **72**, 1259-1268.

1143

1144 119. Garcia-Gonzalez F, Simmons LW. 2010 Male-induced costs of mating for females  
1145 compensated by offspring viability benefits in an insect. *J. Evol. Biol.* **23**, 2066-2075.  
1146

1147 120. Cornwallis CK, Birkhead TR. 2007 Changes in sperm quality and numbers in response  
1148 to experimental manipulation of male social status and female attractiveness. *Am. Nat.* **170**,  
1149 758-770.  
1150

1151 121. Barrett LT, Evans JP, Gasparini C. 2014 The effects of perceived mating opportunities  
1152 on patterns of reproductive investment by male guppies. *PLoS One* **9**, e93780.  
1153

1154 122. Ramm SA, Edward DA, Claydon AJ, Hammond DE, Brownridge P, Hurst JL, Beynon  
1155 J, Stockley P. 2015 Sperm competition risk drives plasticity in seminal fluid composition.  
1156 *BMC Biol.* **13**, 87.  
1157

1158 123. Candolin U, Wong BBM. 2012. Sexual selection in changing environments:  
1159 consequences for individuals and populations *In: Candolin U, Wong BBM (eds) Behavioural*  
1160 *Responses to a Changing World: mechanisms and consequences*. Oxford University Press,  
1161 Oxford, UK. pp 201-215.  
1162

1163 124. Wong BBM, Candolin U. 2014 Behavioural responses to changing environments.  
1164 *Behav. Ecol.* **26**, 665-673.  
1165

1166 125. Slabbekoorn H, Peet M. 2003 Birds sing at a higher pitch in urban noise. *Nature* **424**,  
1167 267.  
1168

1169 126. Slabbekoorn H, den Boer-Visser A. 2006. Cities change the songs of birds. *Curr. Biol.*  
1170 **16**, 2326-2331.  
1171

1172 127. Brumm H. 2013 *Animal Communication and Noise*. Springer Science and Business  
1173 Media. pp453.  
1174

1175 128. Halfwerk W, Bot S, Buikx J, van der Velde M, Komdeur J, ten Cate C, Slabbekoorn H.  
1176 2011 Low-frequency songs lose their potency in noisy urban conditions. *Proc. Nat. Acad. Sci.*  
1177 *USA*. **108**, 14549-14554.  
1178

1179 129. Alberti M, Marzluff J, Hunt VM. 2017 Urban driven phenotypic changes: empirical  
1180 observations and theoretical implications for eco-evolutionary feedback. *Phil. Trans. Roy.*  
1181 *Soc. B*. **372**, 20160029.  
1182

1183 130. Falconer DS, Mackay TFC. 1996 *Introduction to Quantitative Genetics* 4<sup>th</sup> ed.  
1184 Longman, Burnt Mill, UK. pp464.  
1185

1186 131. Holman L, Jacomb F. 2017 The effects of stress and sex on selection, genetic  
1187 covariance, and the evolutionary response. *J. Evol. Biol.* **30**, 1898-1909.  
1188

1189 132. Delcourt M, Blows MW, Rundle HD. 2009 Sexually antagonistic genetic variance for  
1190 fitness in an ancestral and novel environment. *Proc. Roy. Soc. B*. **276**, 2009-2014.  
1191

1192 133. Punzalan D, Delcourt M, Rundle HD. 2014 Comparing the intersex genetic correlation  
1193 for fitness across novel environments in the fruit fly *Drosophila serrata*. *Heredity* **112**, 143-  
1194 148.  
1195  
1196 134. Martinossi-Allibert I, Arnqvist G, Berger D. 2017 Sex-specific selection under  
1197 environmental stress in seed beetles. *J. Evol. Biol.* **30**, 161-173.  
1198  
1199 135. Michelangeli M, Tuomainen U, Candolin U, Wong BBM. 2015 Habitat alteration  
1200 influences male signalling effort in the Australian desert goby. *Behav. Ecol.* **26**, 1164-1169.  
1201  
1202 136. Candolin U, Tukiainen I, Bertell E. 2016 Environmental change disrupts communication  
1203 and sexual selection in a stickleback population. *Ecology* **97**, 969-979.  
1204  
1205 137. Alexander TJ, Vonlanthen P, Seehausen O. 2017 Does eutrophication-driven evolution  
1206 change aquatic ecosystems? *Phil. Trans. Roy. Soc. B.* **372**, 20160041.  
1207  
1208 138. Lande R. 1980 Sexual dimorphism, sexual selection, and adaptation in polygenic  
1209 characters. *Evolution* **34**, 292-305.  
1210  
1211 139. Hoffman AA, Hercus MJ. 2000 Environmental stress as an evolutionary force.  
1212 *Bioscience* **50**, 217-226.  
1213  
1214 140. Charmantier A, Garant D. 2005 Environmental quality and evolutionary potential:  
1215 lessons from wild populations. *Proc. Roy. Soc. B.* **272**, 1415-1425.  
1216



1217 141. Candolin U, Vliieger L. 2013 Should attractive males sneak: the trade-off between  
1218 current and future offspring. *PLoS ONE* **8**, e57992.  
1219

1220 142. Chaine AS, Lyon BE. 2008 Adaptive plasticity in female mate choice dampens sexual  
1221 selection on male ornaments in the lark bunting. *Science* **319**, 459-462.  
1222

1223 143. Candolin U, Salesto T, Evers M. 2007 Changed environmental conditions weaken  
1224 sexual selection in sticklebacks. *J. Evol. Biol.* **20**, 233-239.  
1225

1226 144. Hunt J, Brooks R, Jennions MD, Smith MJ, Bentsen CL, Bussiere LF. 2004. High-  
1227 quality male field crickets invest heavily in sexual display but die young. *Nature* **432**,1024–  
1228 1027.  
1229

1230 145. Zajitschek F, Connallon T. 2017 Partitioning of resources: the evolutionary genetics of  
1231 sexual conflict over resource acquisition and allocation. *J. Evol. Biol.* **30**, 826-838.  
1232

1233 146. van Noordwijk AJ, de Jong G. 1986 Acquisition and allocation of resources – their  
1234 influence on variation in life-history tactics. *Am. Nat.* **128**, 137-142.  
1235

1236 147. Houston AI, McNamara JM. 2002 A self-consistent approach to paternity and parental  
1237 effort. *Phil. Trans. Roy. Soc. B.* **357**, 351-362.  
1238

1239 148. Cotar C, McNamara JM, Collins EJ, Houston A. 2008 Should females prefer to mate  
1240 with low-quality males? *J. Theor. Biol.* **254**, 561-567.  
1241

1242 149. Alonzo SH. 2010 Social and coevolutionary feedbacks between mating and parental  
1243 investment. *Trends Ecol. Evol.* **25**, 99-108.  
1244

1245 150. Kokko H. 1998 Should advertising parental care be honest? *Proc. Roy. Soc. B.* **265**,  
1246 1871-1878.  
1247

1248 151. Alonzo SH. 2012 Sexual selection favours male parental care, when females can choose.  
1249 *Proc. Roy. Soc. B.* **279**, 1784-1790.  
1250

1251 152. Kahn AT, Schwanz LE, Kokko 2013 Paternity protection can provide a kick-start for the  
1252 evolution of male-only parental care. *Evolution* **67**, 2207-2217.  
1253

1254 153. Kelly NB, Alonzo S. 2009 Will male advertisement be a reliable indicator of paternal  
1255 care, if offspring survival depends on male care? *Proc. Roy. Soc. B.* **276**, 3175-3183.  
1256

1257 154. Friberg U, Arnqvist G. 2003 Fitness effects of female mate choice: preferred males are  
1258 detrimental for *Drosophila melanogaster* females. *J. Evol. Biol.* **16**, 797-811.  
1259

1260 155. Harano T. 2015 Receptive females mitigate costs of sexual conflict. *J. Evol. Biol.* **28**,  
1261 320-327.  
1262

1263 156. Cayetano L, Bonduriansky R. 2015 Condition dependence of male and female genital  
1264 structures in the seed beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae). *J. Evol.*  
1265 *Biol.* **28**, 1364-1372.  
1266

- 1267 157. Perry JC, Sirot L, Wigby S. 2013 The seminal symphony: how to compose an ejaculate.  
1268 *Trends Ecol. Evol.* **28**, 414-422.  
1269
- 1270 158. Carazo P, Tan CKW, Allen F, Wigby S, Pizzari T. 2014 Within-group male relatedness  
1271 reduces harm to females in *Drosophila* . *Nature* **505**, 672.  
1272
- 1273 159. Lukasiewicz A, Szubert-Kruszynska A, Radwan J. 2017 Kin selection promotes female  
1274 productivity and cooperation between the sexes. *Sci. Adv.* **3**, e1602262.  
1275
- 1276 160. Kraaijeveld K, Kraaijeveld-Smit FJL, Komdeur J. 2007 The evolution of mutual  
1277 ornamentation. *Anim. Behav.* **74**, 657-677.  
1278
- 1279 161. Clutton-Brock T. 2009 Sexual selection in females. *Anim. Behav.* **77**, 3-11.  
1280
- 1281 162. Fitzpatrick CL, Servedio M. 2018 The evolution of male mate choice and female  
1282 ornamentation: a review of mathematical models. *Curr. Zool.* **64**, 323-333.  
1283
- 1284 163. McLeod DV, Day T. 2017 Female plasticity tends to reduce sexual conflict. *Nature*  
1285 *Ecol. Evol.* **1**, 0054.  
1286
- 1287 164. Day T, McLeod DV. 2018 The role of phenotypic plasticity in moderating evolutionary  
1288 conflict. *Am. Nat.* **192**, 230-240.  
1289
- 1290 165. Rosenthal GG. 2017 *Mate Choice: The Evolution of Sexual Decision-Making from*  
1291 *Microbes to Humans*. Princeton University Press, NJ, USA

1292  
1293  
1294  
1295  
1296  
1297  
1298  
1299  
1300  
1301  
1302  
1303  
1304  
1305  
1306  
1307  
1308  
1309  
1310  
1311  
1312  
1313  
1314  
1315  
1316

166. Cotton S, Small J, Pomiankowski A. 2006 Sexual selection and condition-dependent mate preferences. *Curr. Biol.* **16**, R755-R765.

167. Forstmeier W, Nakagawa S, Griffith SC, Kempenaers B. 2014 Female extra-pair mating: adaptation or genetic constraint? *Trends Ecol. Evol.* **29**, 456-464.

168. Veen T, Otto SP. 2015 Liking the good guys: amplifying local adaptation via the evolution of condition-dependent mate choice. *J. Evol. Biol.* **28**, 1804-1815.

169. Kahn AT, Jennions MD, Kokko H. 2015 Sex allocation, juvenile mortality and the costs imposed by offspring on parents and siblings. *J. Evol. Biol.* **28**, 428-437.

170. Maynard-Smith J. 1982 *Evolution and the Theory of Games*. Cambridge Univ. Press, London, UK.

171. Fromhage L, McNamara JM, Houston AI. 2008 A model for the evolutionary maintenance of monogyny in spiders. *J. Theor. Biol.* **250**, 524-531.

172. Fromhage L, Schneider JM. 2012 A mate to die for? A model of conditional monogyny in cannibalistic spiders. *Ecol. Evol.* **2**, 2572-2582.

173. Hendry AP. 2015 Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *J. Hered.* **107**, 25-41.

1317 174. Booksmythe I, Schwanz LE, Kokko H. 2013 The complex interplay of sex allocation  
1318 and sexual selection. *Evolution* **67**, 673-678.

1319

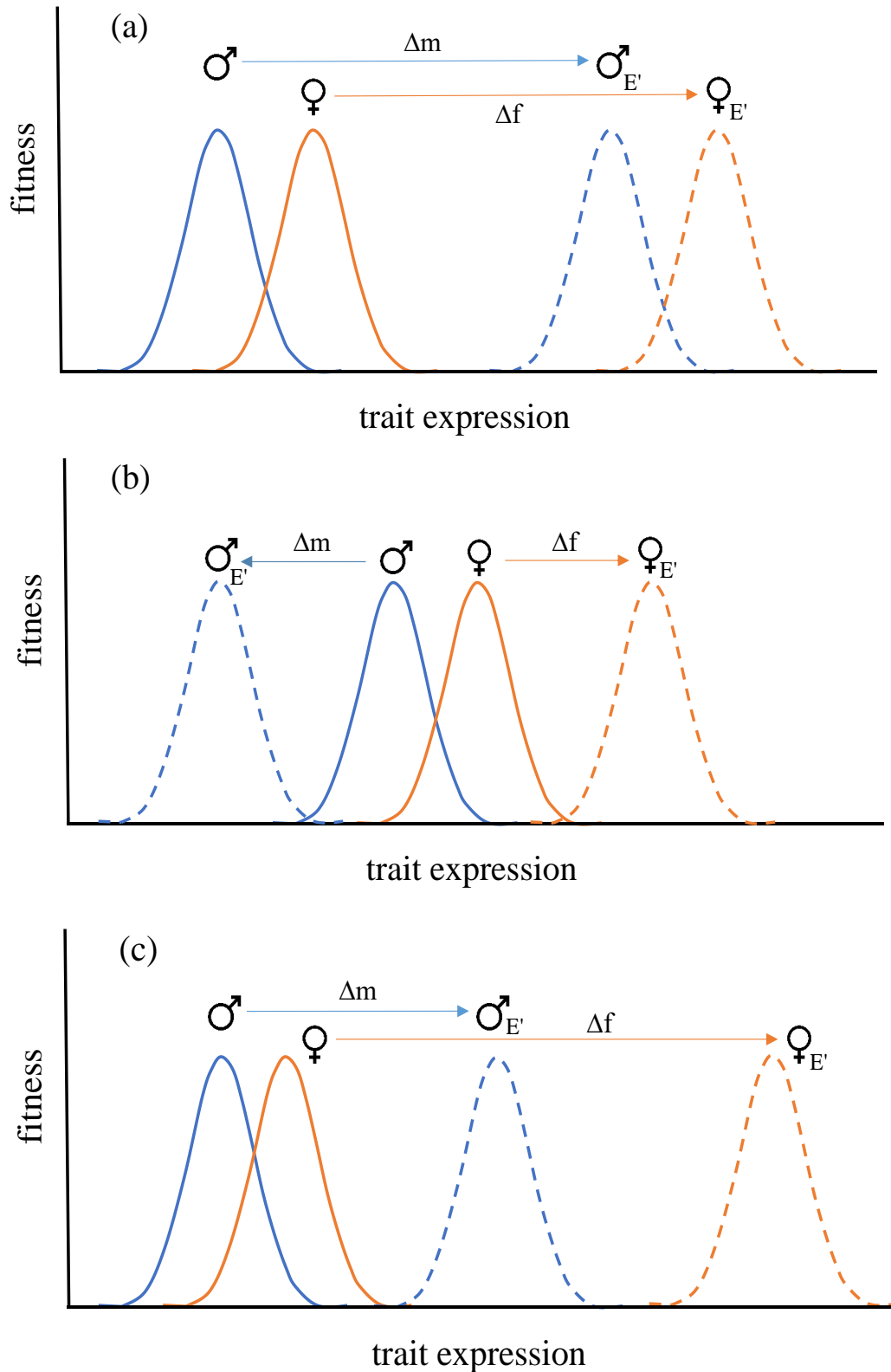
1320 175. Kuijper B, Hoyle RB. 2015. When to rely on maternal effects and when on phenotypic  
1321 plasticity? *Evolution* **69**, 950-968.

1322

1323 176. Hunt J, Hosken D (eds) *Genotype-by-Environment Interactions and Sexual Selection*.  
1324 Wiley-Blackwell.

1325

1326



1328 Figure 1: The likely change in the intersex genetic correlation for fitness ( $r_{MF}$ ) in a changed  
 1329 environment. In the original environment, phenotypic values for males (solid blue) and  
 1330 females (solid orange) are distributed around sex-specific fitness optima. Due to opposing

1331 selection, and in the absence of sex-limited gene expression, the mean phenotype is likely to  
1332 lie between the two optima. In a novel environment (E'), trait optima for each sex shift and,  
1333 following selection, phenotypic values are eventually distributed around the new optima for  
1334 males (dotted blue) and females (dotted orange). (a) shows the 'classic' case in which both  
1335 sexes are displaced in the same direction and by the same amount ( $\Delta m = \Delta f$ ). Genes under  
1336 natural selection in males are therefore likely to benefit females and the inter-sex genetic  
1337 correlation for fitness ( $r_{MF}$ ) is positive. In (b) the novel environment causes the new trait  
1338 optima for each sex to shift in opposite directions (here  $\Delta m = \Delta f$ , but with opposite signs),  
1339 resulting in greater intra-locus sexual conflict i.e.  $r_{MF}$  is negative. Finally, (c) represents a  
1340 case in which the new sex-specific optima are displaced in the same direction, but by  
1341 different amounts (here  $\Delta m < \Delta f$ ), such that  $r_{MF}$ , while briefly positive, becomes more  
1342 negative the further the mean trait value in the population surpasses the new male optimum.