

1 **In review.**

2

3 **Natural selection reverses the exaggeration of a male sexually selected**
4 **trait, which increases female fitness.**

5

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30 M.K., K.K., Y.O., and MDS conducted experiments; KO, MDS, AJW analyzed data; and
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35 **Key words: sexual selection, predation, sexual conflict, genetic correlation, fitness**

36 **Abstract**

37 Theory shows how sexual selection can exaggerate male traits beyond naturally selected
38 optima and also how natural selection can ultimately halt trait elaboration. Empirical
39 evidence supports this theory, but to date, there have been no experimental evolution
40 studies directly testing this logic, and little examination of possible associated effects on
41 female fitness. Here we used experimental evolution of replicate populations of
42 broad-horned flour-beetles to test for evolutionary effects of sex-specific predation on
43 an exaggerated sexually selected male trait, while also testing for effects on female
44 lifetime reproductive success. We found that populations subjected to male-specific
45 predation evolved smaller sexually selected traits and this indirectly increased female
46 fitness, seemingly through intersexual genetic correlations we documented. Predation
47 solely on females had no effects. Our findings support fundamental theory, but also
48 reveal novel outcomes when natural selection targets sex-limited sexually selected
49 characters.

50 **Introduction**

51 Sexual selection typically acts more strongly on males and is responsible for the
52 evolution of a vast array of exaggerated characters that enhance male sexual fitness
53 components (Andersson 1994; Shuster & Wade 2003; Andersson & Simmons 2006;
54 Hosken & House 2011). Lande's (1981) and Kirkpatrick's (1982) models of sexual
55 selection via the Fisher (1930) process – the null models of intersexual selection (Prum
56 2010) – clearly shows how this can occur. They also demonstrates how natural selection
57 can oppose sexual selection as trait values move beyond their naturally selected optima
58 (reviewed in Arnold 1983). While theory is clear on the joint effects of natural and
59 sexual selection on sexual trait evolution, explicit experimental tests of theoretical
60 predictions are required to fully understand sexual trait evolution (Pocklington & Dill
61 1995).

62

63 One potentially important source of natural selection that could affect the evolution of
64 sexually selected traits is predation (Andersson 1994), and many studies have shown
65 predation can seemingly oppose the exaggeration of male sexual characters. For
66 example, sexual signals are conspicuous to potential mates but may also attract
67 predators and parasitoids (Zuk & Kolluru 1998). This is well documented in
68 orthopterans and frogs (e.g. Cade 1975; Ryan et al. 1982; Sakaluk & Belwood 1984;
69 Ryan 1985; Hosken et al. 1994; Rotenbury et al. 1996; Gray & Cade 1999), and this
70 form of natural selection is probably responsible for the loss of cricket sexual signals on
71 two Hawaiian islands (Zuk et al. 2006; Pascoal et al. 2014). More generally, predation
72 appears reverse the evolution of extreme sexually selected phenotypes (reviewed in
73 Kotiaho 2001) and males frequently reduce their sexual signaling in response to

74 predation risk, which can result in decreased mating success when risk is high (Lima
75 and Dill 1990; Sakaluk 1990; Candolin 1998; Kotiaho et al. 1998). Nonetheless, while
76 there is ample evidence that predation selects against sexual trait enhancement, there is
77 limited direct experimental verification that this generates evolutionary responses in
78 these characters (but see e.g. Zuk et al. 1993; Millar et al. 2006).

79

80 Female reproductive success can also be impacted by predation (Reznick et al. 1990;
81 Magnhagen 1991). For example, egg-carrying females can be slower (Cooper et al.
82 1990; Berglund and Rosenqvist 1986) and suffer higher predation rates (Lee et al. 1996;
83 Magnhagen 1991). Resultant anti-predator behaviours may reduce foraging efficiency
84 and reproductive activity, and thus be costly to females (reviewed in Lima and Dill
85 1990). Costs can be generated by delayed development, slower growth or postponed
86 reproduction (Barry 1994; Clobert et al. 2000; Koskela and Ylönen 1995; Lind &
87 Cresswell 2005). Nonetheless, while there is ample evidence that predation selects on
88 both sexes, selection on females and males is frequently investigated independently, and
89 again the evolutionary effects of any sex-specific selection are frequently inferred. That
90 is, controlled experimental tests of evolutionary responses to this selection are usually
91 not undertaken. Unfortunately, without exploring how predation affects both sexes, we
92 are unlikely to fully understand how predation affects sexual trait evolution
93 (Pocklington & Dill 1995). This is especially true when intersexual genetic correlations
94 link sexually selected male characters with female fitness because selection on one sex
95 can affect the other via these correlations.

96

97 Here we tested for effects of predation on the evolution of a male sexually selected

98 character and female lifetime reproductive success (LRS) in the broad-horned flour
99 beetle *Gnaticerus cornutus*. Male beetles develop enormously enlarged mandibles that
100 are used in male-male fights, and males with larger mandibles have higher fighting and
101 mating success (Okada & Miyatake 2009; Harano et al. 2010). Females lack this
102 exaggerated character completely (Okada et al. 2006). We have previously shown that
103 males with larger mandibles sire daughters with lower fecundity, and that selecting for
104 increased (or decreased) mandible size results in decreased (or increased) female fitness
105 (LRS) (Harano et al. 2010). This apparently occurs because of the beetle's genetic
106 architecture, which means evolving larger mandibles results in the correlated evolution
107 of masculinized females (even though females never develop mandibles). Basically, the
108 enlarged male mandible requires a masculinised head and prothorax to function
109 optimally and this means males with larger mandibles have smaller abdomens (Harano
110 et al. 2010; Okada et al. 2012). Thus although females never develop mandibles,
111 selecting on male mandibles ultimately affects female abdomen size, which likely
112 determines the number of eggs a female carries (Harano et al. 2010, and also see Honěk
113 1993). These previous *G. cornutus* studies clearly document intralocus sexual conflict
114 over beetle morphology (e.g. Harano et al. 2010; Katsuki et al. 2012b) and point to a
115 negative intersexual correlation between (male) mandible size and female fitness,
116 although this link has not been directly established and requires confirmation (c.f.
117 Pennell et al. 2016). With this in mind we investigated the beetle's intersexual genetic
118 architecture for key focal traits using an animal model (Wilson et al. 2010). We also
119 established replicate (3/treatment) experimental evolution populations subjected to
120 either male or female predation, along with control populations (n = 3, for 9 total
121 populations). After 8 generations of experimental evolution, we assessed female fitness

122 (LRS) and measured a range of morphological characters, including mandible size.
123 Morphology was also measured during experimental evolution. We found strong effects
124 of male-specific predation on morphology and female fitness, while predation on
125 females alone had no effects.

126

127 **Results**

128 The genetic parameters estimated from the animal model analyses confirmed what
129 previous experimental evolution studies had inferred (e.g. Okada & Miyatake 2009;
130 Harano et al. 2010). Likelihood ratio comparisons of univariate models confirmed the
131 presence of additive genetic variance in all four traits (supplemental materials) as
132 expected. Note that the decision to treat the two mass measures as the same trait across
133 the sexes was justified by an absence of significant genotype-by-sex interaction in
134 univariate models. Cross-sex genetic correlations were estimated as c.+1 for both traits,
135 but we do note there is a qualitative pattern of higher additive variance for body mass in
136 females (see supplemental materials for these analyses and some further comment).

137 Multivariate models further confirmed the presence of additive genetic variance (LRT
138 comparison of null model to one with a diagonal genetic matrix; $\chi^2_4=74.96$, $P<0.0001$),
139 as well as significant among-trait genetic correlation structure (LRT comparison of
140 model with a diagonal genetic matrix to full model with all genetic correlations
141 included; $\chi^2_6=39.02$, $P<0.0001$). Parameter estimates from the full multivariate model
142 show substantial genetic variation in all traits measured and reasonably high trait
143 heritability (Table 1). All traits were positively genetic correlated except male
144 mandible size and female fitness (lifetime reproductive success) and male mandible size
145 and abdominal mass, which were both strongly negatively correlation. Individual

146 genetic correlations were nominally significant at $\alpha=0.05$ (based on $|r_G| > 1.96SE$)
147 except between body and abdomen mass and between body mass and female LRS.

148

149 The experimental treatments we imposed on the replicated beetles populations
150 generated treatment specific evolutionary responses in some traits but not others (Figure
151 1). When we compared trait values at the end of the experimental evolution period we
152 found that predation significantly affected male mandible size (Figure 2a. $F_{2,6} = 31.07$;
153 $P < 0.001$). *Post-hoc t*-tests [with sequential Bonferroni adjustment] revealed that when
154 males were exposed to predators they evolved the smallest mandibles (all $P < 0.01$),
155 while the control and female treatments did not differ in mandible size ($P = 0.36$).
156 Similarly, predation effected male abdomen size ($F_{2,6} = 31.04$; $P < 0.001$), and *post-hoc*
157 *t*-test revealed that males exposed to predators evolved the largest abdomens (all $P <$
158 0.01) while control and female predator-exposure treatments did not differ ($P = 1.0$)
159 (Figure 2b). Total male body size was unaffected by our treatments (Figure 2c: $F_{2,6} =$
160 1.17 ; $P = 0.373$).

161

162 Predation also effected female LRS (Figure 2d: $F_{2,6} = 21.29$; $P = 0.002$). *Post-hoc*
163 *t*-tests showed that this was because in the male predation treatment female fitness was
164 higher (all $P < 0.01$), while the other treatments did not differ (control = female
165 predation: $P = 0.54$). Thus exposing males to predators resulted in the evolution of
166 smaller male mandibles and higher female fitness. As with males, female abdomen
167 size was impacted by our treatments ($F_{2,6} = 10.75$; $P = 0.010$) and again the male
168 predator exposure group evolved the largest female abdomens (all $P \leq 0.01$: control =
169 female predation $P = 1.0$). Finally, female body size was unaffected by our

170 experimental regimes ($F_{2,6} = 1.65$; $P = 0.269$).

171

172 To summarise the main findings: male-specific predation results in an altered, more
173 feminized male phenotype, that included reductions in the size of a male-limited
174 sexually selected trait. Additionally, because of the beetle's genetic architecture, the
175 "new" demasculinized male phenotype was transmitted through to the female
176 phenotype and resulted in higher fitness females (Figure 3).

177

178 **Discussion**

179 Predation is frequently invoked as an evolutionary brake on the exaggeration of
180 sexually selected traits and there are many studies consistent with this logic, usually
181 documenting selection against larger characters or assessing macro-evolutionary
182 patterns consistent with it (e.g. Zuk et al. 1993; Millar et al. 2006). Here we employed
183 experimental evolution and directly demonstrate that male-specific predation not only
184 reversed the exaggeration of a sexually selected trait, but additionally, this reversal
185 resulted in higher female fitness. This boost to female fitness occurred because
186 predators selecting against mandible enlargement in males results in a less masculinized
187 phenotype (a larger abdomen), and because of shared genetic architecture across the
188 sexes, this allows females to become more feminized and produce more offspring. We
189 discuss these findings in turn.

190

191 When males were exposed to predation, they evolved smaller mandibles. Thus
192 increased natural selection via predation reduced the size of a sexually selected trait,
193 which is broadly consistent with theory (e.g. Lande 1981; Kirkpatrick 1982; reviewed in

194 Andersson 1994). Previous work with *G. cornutus* suggests why this occurred.
195 Mandible size is negatively phenotypically and genetically associated with locomotor
196 activity (Fuchikawa and Okada 2013), and locomotor activity (running) is a predator
197 escape mechanism in flour beetles (Miyatake et al. 2008). Reduced running and lower
198 escape rates for males with large mandibles would explain the microevolutionary
199 pattern we detected. Interestingly, there is no intersexual correlation for locomotion in
200 this beetle (Fuchikawa and Okada 2013), so there was no expectation that predation on
201 females should impact male running speed and hence morphology. Be that as it may,
202 we clearly showed that natural selection reversed the evolutionary exaggeration of a
203 sexually selected male trait.

204

205 Females from the male-predation populations evolved higher fitness (LRS) even though
206 females were not directly exposed to predators. Harano et al. (2010) demonstrated that
207 directly artificially selecting for larger (male) mandibles reduces female fitness. This
208 occurred because selection for increased mandible size resulted in a more masculinized
209 phenotype and this masculinization ripples through inferred intersexually-shared genetic
210 architecture to increase the masculinization of the female phenotype, reducing female
211 fitness. The intersexual genetic associations we documented here, especially the
212 negative mandible-female LRS correlation, flesh out this explanation and confirm
213 previous inference (Harano et al. 2010). Negative intersexual fitness associations are
214 common (Arnqvist & Rowe 2005; Bonduriansky & Chenoweth 2009) because alleles
215 conferring high fitness to one sex frequently lower fitness in the other (e.g. Chippindale
216 et al. 2001; Rostant et al. 2015). In addition to any sexually antagonistic selection, male
217 beetles with larger mandibles are also more aggressive toward females (Kiyose et al.

218 2015). Thus exposure to males with larger mandibles potentially reduces female LRS
219 due to (misdirected) male attacks (Kiyose et al. 2015). Therefore there could be two
220 avenues to increased female fitness when predators select against large male mandibles,
221 a reduction in ontogenetic conflict load (intra-locus sexual conflict load), or reduced
222 aggression. In any case, predation caused an evolutionary reduction in mandible size
223 and this resulted in increased female fitness. Thus male-biased predation indirectly
224 selects for increased female quality.

225

226 The net population level effects of sexual selection and sexual conflict over optimal
227 phenotypes are not clear (e.g. Kokko and Brooks 2003; Arnqvist & Rowe 2005), with
228 for example, evidence that sexual selection can both increase and decrease population
229 extinction rates (e.g. Doherty et al. 2003; Jarzebowska & Radwan 2010; Lumley et al.
230 2015). Additionally, intra-locus sexual conflict (as documented in the flour beetle:
231 Harano et al. 2010) is thought to constrain population adaptation because sexually
232 antagonistic selection keeps each sex from its fitness optima (Rice 1992; Arnqvist &
233 Rowe 2005). Our results suggest that predator purging of males with the largest sexual
234 traits reduces intra-locus (ontogenetic) sexual conflict costs, enhancing female
235 reproductive performance, which should (all else being equal) increase population
236 productivity. Relaxing other sexual conflict can also increase population fitness (e.g.
237 Holland & Rice 1999; Martin & Hosken 2004). It is interesting to note that predators
238 are usually seen as suppressing prey populations (Nelson et al. 2004), which can have
239 indirect ecological benefits for prey competitors (e.g. Paine 1966). As we have shown,
240 sex-biased predation can have analogous indirect effects intra-specifically. However,
241 the indirect impacts we documented were unidirectional since female-biased predation

242 did not alter female fitness or male sexual-trait size.

243

244 Negative intersexual correlations for fitness are an indicator of intralocus sexual conflict
245 (Bonduriansky & Chenoweth 2009) - although this can be complicated by *Wolbachia*
246 infection (Duffy et al. 2019) - and we find negative correlations for fitness surrogates
247 here – mandible size determines male fitness and LRS reflects female fitness (e.g.
248 Harano et al. 2010; Katsuki et al. 2012b; Okada et al. 2014). Regardless of arguments
249 about fitness and fitness correlates, this negative association provides the genetic link to
250 correlated responses to selection on mandible size previously documented (e.g. Harano
251 et al. 2010) and to those we see here.

252

253 Overall this study provides direct evidence that predator-mediated natural selection can
254 evolutionarily reverse the exaggeration of a sexually selected trait. This finding is
255 consistent with a vast body of fundamental theory (e.g. Lande 1981; Kirkpartick 1982;
256 Hall et al. 2000) and empirical evidence (e.g. Zuk et al. 2006; reviewed in Andersson
257 1994). We also reveal novel outcomes when natural selection targets sex-limited
258 sexually selected characters, since predator removal of a male imposed conflict load
259 increased female fitness. Thus sex-biased predation within a species can essentially
260 mimic indirect ecological competition effects. Investigating the precise mechanistic
261 detail of some of these findings is now required.

262

263

264 **Methods**

265 ***Gnatocerus* stock culture**

266 The *G. cornutus* beetle culture originated from adults collected in Miyazaki City (31°
267 54'N, 131° 25' E), Japan, and has been maintained in the laboratory of the National
268 Food Research Institute, Japan, for about 50 years on whole meal enriched with yeast as
269 food. The stock is made up of 1500-2000 beetles per generation and maintained in
270 plastic cups (diameter 95 mm, height 50 mm) with a standing density of between 300
271 and 400 beetles per cup (for a more detailed description of the stock culture, see Okada
272 & Miyatake (2010)). This beetle is a stored product pest, and thus the laboratory
273 conditions very closely mimic what have become their natural conditions. Virgin males
274 and females were removed from the stock population as final instar larvae. Each larva
275 was placed in one well of a 24-well tissue culture plate (Cellstar; Greiner Bio-One,
276 Frickenhausen, Germany) until adult eclosion because pupation in *G. cornutus* is
277 inhibited under high larval density (Okada & Miyatake 2010). After eclosion, both
278 sexes were allowed to sexually mature for a period of 14 days prior to their use. We
279 performed all rearing and experiments in a chamber maintained at 25°C, 60% relative
280 humidity, and with a photoperiod cycle of 14:10 h light/dark. All experiments in this
281 study follow this protocol unless stated otherwise.

282

283 **The predator**

284 The assassin bug *Amphibolus venator* is predator of stored-product insect pests and
285 preys on various stored-product insect pests including flour beetles (Pingale 1954; Nishi
286 and Takahashi, 2002; Imamura et al. 2008). These predators are frequently found in
287 stored product facilities, which are the habitat of *G. cornutus* (Nishi & Takahashi, 2002).
288 The *A. venator* culture originated from adults collected in a storehouse in Urasoe City,
289 Okinawa, Japan, and has been maintained in the laboratory for about 5 years. The stock

290 was initiated and maintained at 200 bugs per generation and housed in plastic containers
291 (230 mm × 150 mm × 80 mm) with a standing density of between 30 and 40 bugs per
292 cup. Each nymph was given an excess of food (7 final instar larvae of *G. cornutus* per
293 week). Each adult female was allowed to mate with a male chosen randomly and to lay
294 eggs in order to maintain the predator stocks.

295

296 ***Gnatocerus* breeding design and estimation of quantitative genetic parameters**

297 Using a full sib/half sib experimental design, males (sires) (N = 35) were randomly
298 assigned to three virgin females (dams) (all collected from the stock population). Pairs
299 were housed in a plastic container (17 mm diameter, 20 mm high) containing filter
300 paper (17 mm diameter), and successful copulation was indicated by a stable end-to-end
301 connection between the male and female. After mating, dams were immediately
302 removed and individually placed in a plastic cup (70 mm diameter, 25 mm high)
303 containing excess food (20 g). Each female was housed thus for two months to obtain
304 offspring. All offspring from each female were reared to final instar (approximately 8
305 weeks). Three sons and three daughters per dam per sire were haphazardly chosen for
306 measurement of male traits (mandible, body and abdomen size) and female traits (LRS,
307 body and abdomen size) at 14 days after eclosion (N = 315 per sex) (trait measurement
308 protocols below).

309

310 Data from the breeding design were then analysed using pedigree-based animal models
311 fit in ASReml-R (Butler et al. 2017). First, to confirm the presence of additive genetic
312 variance in each trait we fit a series of univariate animal models to (male) mandible,
313 body and abdomen size, and to female (LRS). For each trait we compared the model fit

314 to a reduced model with no additive genetic effects using a likelihood ratio test (LRT;
315 adjusted for boundary conditions following Stram & Lee (1994)). We elected to
316 combine male and female records for both body size and abdomen sizes as additional
317 modelling provided little support for genotype-by-sex interactions (see results).
318 However, for these traits a fixed effect of sex was included, as well as the (random)
319 additive genetic effect since exploratory analysis showed sexual dimorphism in both
320 traits (body size, males are 0.020 mg (SE 0.005) larger on average, $t=3.58$, $P<0.001$;
321 abdomen size, males are 0.019 mg (SE 0.008) smaller on average, $t=2.463$, $P=0.014$)).

322

323 We then fitted a multivariate animal model to estimate genetic correlation (r_G) structure
324 among the four traits with fixed effects of sex on body size, abdomen size, as well as
325 their heritability (h^2). The residual covariance structure was modelled as an unstructured
326 matrix (but note residual covariance between the sex limited traits of male mandible
327 size and female LRS is not estimable from the data so was fixed to zero). We also ran
328 reduced multivariate models with i) no genetic effects at all, and ii) a diagonal genetic
329 variance matrix (i.e. genetic variance modelled on all traits but all genetic correlations
330 assumed to equal zero) for comparison to the full model by LRT. This allows statistical
331 inference at the level of the multivariate phenotype. We used estimated standard errors
332 (SE) as a guide to nominal significance of pairwise genetic correlations (assuming
333 approximate 95% CI are given by $r_G \pm 1.96SE$).

334

335 ***Gnatocerus* experimental evolution protocol – sex specific predation**

336 We first collected 900 male and 900 female *G. cornutus* from the stock culture and
337 haphazardly generated 9 groups of 100 males and 100 females to establish three

338 male-predation populations, three female-predation populations and three control (no
339 predation) populations (generation 0). To simulate predation, 100 males (or females)
340 were housed in a plastic container (150 mm diameter, 50 mm high) containing an excess
341 of beetle food (45 g). Then, five adult female *A. venator* (20-35 day olds) were
342 randomly collected from the predator culture and placed into the container and the
343 males (females) were exposed to them for two weeks. We then selected 10 of the males
344 (females) that survived the two weeks to act as sires (dams) of the predation treatments -
345 10 opposite sex individual were also taken/population to act as the non-selected dams
346 (sires) that were not exposed to predation. We note that survival rate during this
347 predation protocol was approximately 20%. To propagate control populations, 10 males
348 and 10 females were haphazardly selected per population to act as sires and dams. For
349 each population/treatment the 10 males and females were placed in a plastic cup
350 (diameter 95 mm, height 50 mm) with 70 g of medium for two months, with males able
351 to mate with females and females were allowed to lay eggs, until final instar larvae were
352 obtained. Final instar larvae were collected to obtain the adults for subsequent
353 generations. When the adults reached 14 days old, 100 males and 100 females per
354 population were randomly selected to (potentially) seed the next generation, and in the
355 predation treatments, exposed to predators as above. We then selected surviving animals
356 as above and repeated for 8 generations. Additionally, we also collected 50 males and
357 50 females per population from generation 1 to 7 to assess mandible, abdomen and body
358 size responses to selection. At generation 8, 20 males and 20 females per population
359 were haphazardly collected for measurement of male traits (mandible, body and
360 abdomen size) and female traits (LRS, body and abdomen size) (N = 180 per sex) (trait
361 measurement protocols below).

362

363 **Male trait measurement**

364 We measured overall body mass and the posterior body mass (i.e., mesothorax,
365 metathorax, and abdomen) as an abdomen size indicator (see Harano et al. 2010).
366 Briefly, each male was frozen at -20 °C immediately after adult emergence. Mass
367 measures were obtained to the nearest 0.01 mg on an electronic balance (Mettler-Toledo
368 AG, Laboratory and Weighing Technologies). The mandible length (± 0.01 mm) of each
369 male was measured (± 0.01 mm) using a dissecting microscope monitoring system
370 (VM-60; Olympus, Tokyo, Japan). Each specimen was positioned so that its
371 longitudinal and dorsoventral axes were perpendicular to the visual axes of the
372 microscope eyepiece (see Okada & Miyatake, 2010 for landmarks).

373

374 **Female trait measurement**

375 To obtain LRS (lifetime reproductive success: our fitness proxy) each female (14 days
376 post-eclosure) was individually paired with a haphazardly selected male from the stock
377 culture. After copulation, each female was maintained in a plastic cup (70 mm diameter,
378 25 mm high) containing an excess of with food (20 g) for two months and allowed to
379 lay eggs. This schedule was chosen because most eggs are laid by females within two
380 months of mating (Tsuda and Yoshida 1984), and thus this is an accurate index of LRS
381 (Katsuki et al. 2012ab). To measure the LRS of each female, we counted all adults that
382 emerged in the third month after pairing. After the laying period, each female was
383 frozen at -20 °C. Subsequently, the whole and posterior of the body (body size and
384 abdomen size) were weighed with the electronic balance (as above).

385

386 Apart from the genetic parameter estimation with an animal model (using ASReml-R as
387 described above), all analyses were conducted using JMP for Windows version 8 (SAS
388 Institute 2008). We used population as the unit of replication (= 9 DF max.) with single
389 fixed factor (with 3 levels: the experimental treatments) GLMs for each trait to test for
390 effects of experimental evolution, with post-hoc testing for factor-level differences (note
391 we did not have sufficient DF for a multivariate analysis). Results are as reported even
392 after (conservative: Nakagawa 2004) sequential Bonferroni correction.

393

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397

398 **Declaration of interests.**

399 The authors have no interests to declare.

400

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- 566

567 **Table 1.** Estimates of the genetic variance-covariance structure among traits in the
 568 breeding design. Estimates are shown standardized to narrow sense heritability (h^2 ;
 569 shaded diagonal) and genetic correlations (r_G ; above diagonal). Values were estimated
 570 using a four trait animal model with body and abdomen mass treated as the same trait in
 571 both sexes (but with sex as a fixed effect). Standard errors are denoted in parentheses
 572 and bold font denotes estimates that are nominally significant at $P < 0.05$ assuming
 573 approximate 95% CI are provided by the estimate ± 1.96 SE.

574

Traits	Body mass	Abdominal mass	Male mandible size	Female LRS
Body mass	0.346 (0.085)	0.296 (0.164)	0.574 (0.162)	0.422 (0.242)
Abdominal mass		0.513 (0.096)	-0.415 (0.171)	0.596 (0.199)
Male mandible size			0.380 (0.111)	-0.598 (0.250)
Female LRS				0.214 (0.106)

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578

579 **Figure Legends.**

580 **Figure 1.** Responses to selection on predation in male mandible size (mm) (a), male
 581 abdomen size (mg) (b), male body size (mg) (c), female abdomen size (mg) (d) and
 582 female body size (mg) (e) (mean \pm SE). White circles are the control populations that
 583 were not subjected to selection by predation. Black squares and triangles, are the
 584 populations with male and female exposure to predators, respectively. Note we did not
 585 measure female fitness (lifetime reproductive success: LRS) at every generation as it
 586 was not logistically possible.

587

588 **Figure 2.** Trait values after 8 generation of experimental evolution. Replicate
589 populations (3/treatment) were exposed to either male-only predation (middle columns),
590 female-only predation (right-hand columns) or no predation (controls: left-hand
591 columns), and effects on a range of traits was assessed. Traits were: Male mandible size
592 (mm) (a), Male abdomen size (mg) (b), Male body size (mg) (c), Female lifetime
593 reproductive success (LRS: offspring number) (d), Female abdomen size (mg) (e) and
594 Female body size (mg) (f) (shown are means (population as replicate) \pm SE).

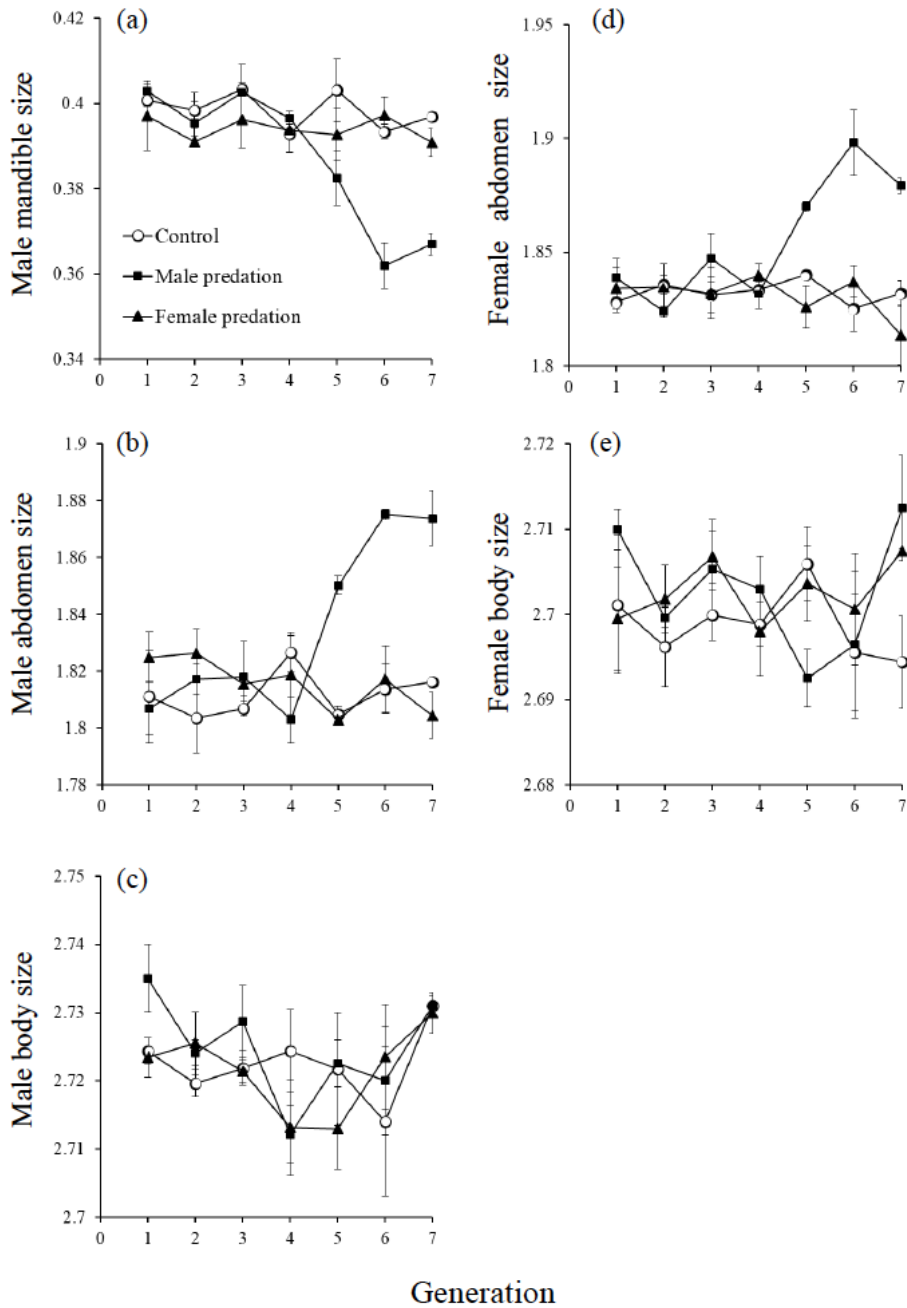
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597 **Figure 3.** A diagrammatic representation of the male and female phenotypes resulting
598 from male-limited predation in comparison to those resulting from sexual selection on
599 males. Sexual selection (left images) results in enlarged male mandibles, which require
600 a masculinized head and prothorax to operate effectively. This fore-body
601 masculinization results in a smaller male abdomen and because of intersexual
602 correlations for abdomen size, a smaller female abdomen and capacity for fewer eggs,
603 even though females never develop mandibles. Male-limited predation selects against
604 the masculinized phenotype, ultimately resulting in larger male and female abdomens,
605 and hence more eggs and higher fitness females (images on the right).

606 **Figure 1**

607



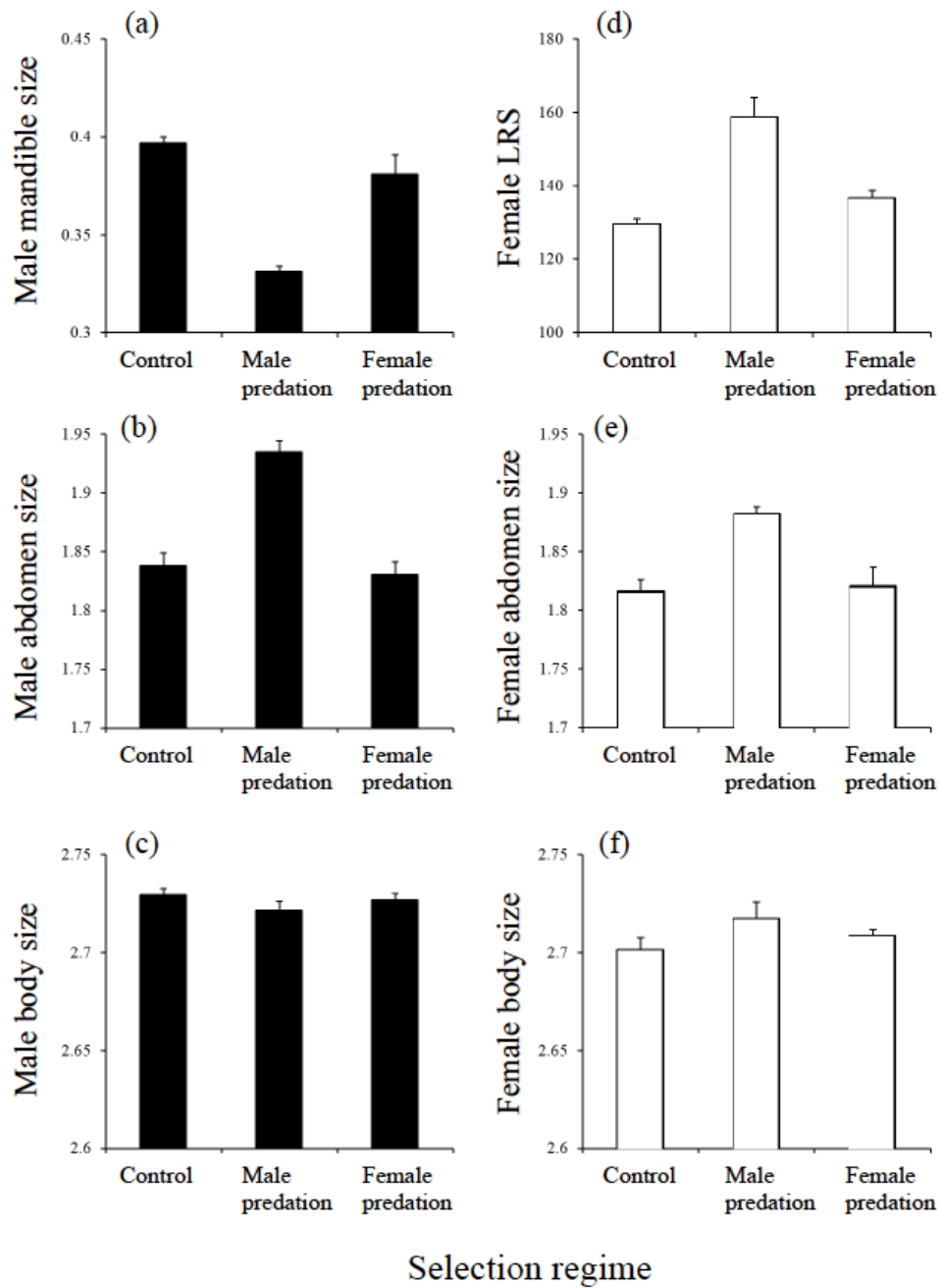
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611 Figure 2.

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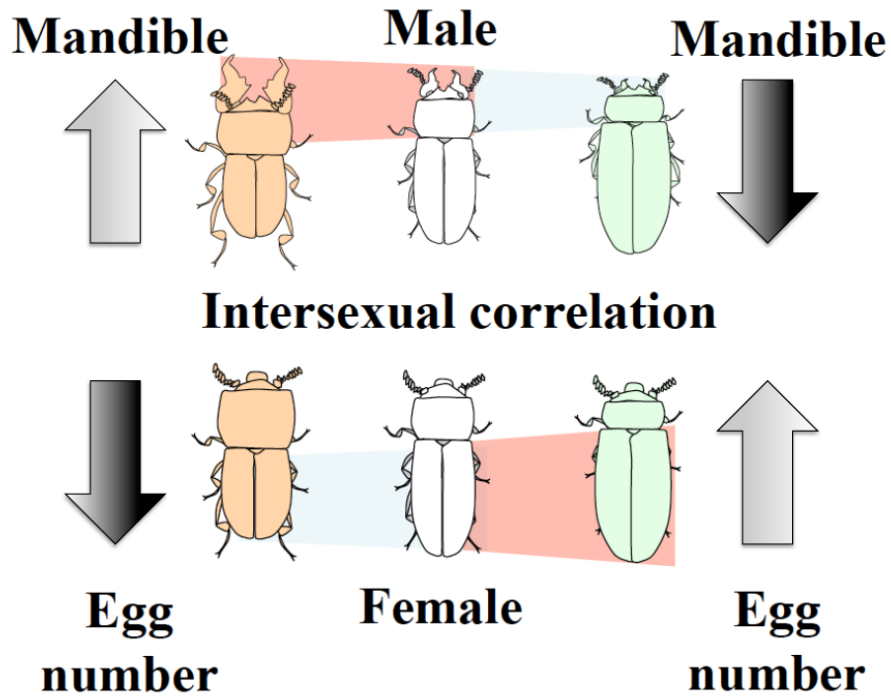
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616 Figure 3.

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Sexual selection

Male predation



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622 **Supplementary Information**

623

624 **Estimated fixed effects and heritabilities from univariate animal models of**
 625 **each trait.** Body mass and abdomen mass were treated as single traits rather than
 626 sex-specific ones, with sex included as a fixed factor. Statistical inference on fixed effects
 627 is by conditional F test while the presence of additive genetic variance was tested by
 628 LRT comparison to a reduced model assuming twice the difference in model
 629 log-likelihoods is distributed as a 50:50 mix of X^2_0 and X^2_1 .

630

631

Trait	Fixed effects		DF	F	P	Random effects		
	Effect	Estimate (SE)				h^2 (SE)	$X^2_{0,1}$	P
Body mass	mean	2.701 (0.005)	1,50.9	318800	<0.001	0.343 (0.085)	33.95	<0.001
	Sex (male)	0.020 (0.005)	1,528.7	15	<0.001			
Abdomen mass	mean	1.843 (0.008)	1,57.2	55940	<0.001	0.508 (0.096)	58.11	<0.001
	Sex (male)	-0.019 (0.007)	1,523.0	8	0.005			
Male mandible length	mean	0.396 (0.004)	1,44.0	10050	<0.001	0.286 (0.121)	8.50	0.002
Female LRS	mean	141.873 (1.714)	1,41.8	6849	<0.001	0.165 (0.108)	3.234	0.036

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634

635 **Tests for genotype-by-sex interaction in body and abdomen mass.** Shown are
 636 likelihood ratio test (LRT) comparisons of a simple univariate animal model (including a
 637 fixed effect of sex) to once in which genotype-by sex interaction is modelled. Twice the
 638 difference in log-likelihoods is assumed to be distributed as X^2 with 2DF. Also shown are
 639 estimates of genetic variance (V_A) under the simple model and the sex-specific genetic
 640 variances (V_{Af} , V_{Am}) and the cross-sex genetic correlation (r_{Gmf}) under the expanded
 641 model allowing genotype-by-sex interaction. Standard errors are shown in parentheses

642 where available. Note that to keep the genetic variance-covariance matrix in allowable
 643 parameter space (i.e. positive definite) r_{Gmf} was bound to (effectively) +1 in both
 644 expanded models and no SE is estimated as a consequence. For body mass the
 645 improvement to model fit is marginally non-significant when the
 646 genotype-by-environment interaction is included. To the extent this might reflect real
 647 differences in sex-specific genetic architecture the pattern is driven by apparent
 648 differences in V_A across the sexes (rather than deviation from $r_{Gmf}=1$). Consequently, we
 649 assuming an absence of genotype-by-sex interaction for this trait, we also note that the
 650 estimated heritability presented in the main manuscript remains valid (as an average
 651 across the sexes) even if this assumption is incorrect.

Trait	Model comparison		Simple animal model	Expanded model with genotype-by-sex interaction		
	X^2_2	P	V_A (SE)	V_{Af} (SE)	V_{Am} (SE)	r_{Gmf}
Body mass	5.49	0.075	0.0017 (0.0005)	0.0026 (0.0006)	0.0013 (0.0005)	0.9999
Abdomen mass	0.20	0.915	0.0050 (0.0012)	0.0053 (0.0014)	0.0047 (0.0013)	0.9999

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653