

1 **Title:** Intralocus sexual conflict can maintain alternative reproductive tactics

2 **Running Title:** Sexual conflict maintains ARTs

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13

14 **Abstract**

15 Alternative reproductive tactics (ARTs) are ubiquitous throughout the animal kingdom and
16 widely regarded as an outcome of high variance in reproductive success. Proximate mechanisms
17 underlying ARTs include genetically based polymorphisms, environmentally induced
18 polymorphisms, and those mediated by a combination of genetic and environmental factors.
19 However, few ultimate mechanisms have been proposed to explain the maintenance of ARTs
20 over time, the most important of which have been disruptive and negative frequency-dependent
21 selection. Here we explore the role that intralocus sexual conflict may play in the maintenance of
22 sex-specific ARTs. We use a genetically explicit individual-based model in which body size
23 influences both female fecundity and male tactic through a shared genetic architecture. By

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24 modeling ART maintenance under varying selection regimes and levels of sex-specific gene
25 expression, we explore the conditions under which intralocus sexual conflict can maintain a
26 hypothetical ART defined by larger (alpha) and smaller (beta) tactics. Our models consistently
27 revealed that sexual conflict can result in the persistence of a sex-specific polymorphism over
28 hundreds of generations, even in the absence of negative frequency-dependent selection. ARTs
29 were maintained through correlated selection when one male ART has lower fitness but produces
30 daughters with higher fitness. These results highlight the importance of understanding selection
31 on both sexes when attempting to explain the maintenance of ARTs. Our results are consistent
32 with a growing literature documenting genetic correlations between male ARTs and female
33 fitness, suggesting that the maintenance of sex-specific ARTs through intralocus sexual conflict
34 may be common and widespread in nature.

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35 **Introduction**

36 Alternative reproductive tactics (ARTs) are ubiquitous throughout the animal kingdom and
37 are widely regarded as an outcome of high variance in reproductive success (Shuster and Wade
38 2003). Proximate mechanisms underlying ARTs include purely genetically based polymorphisms
39 (Shuster 1989; Cordero 1990; Lank et al. 1995; Sinervo and Lively 1996; Sinervo et al. 2000b),
40 purely environmentally induced polymorphisms (Thornhill 1981; Emlen 1994; Hunt and
41 Simmons 1997; Moczek and Emlen 1999), as well as those mediated by a combination of genetic
42 and environmental factors (Neff and Svensson 2013). However, few ultimate mechanisms have
43 been proposed to explain the evolutionary maintenance of ARTs over time. The most prominent
44 of these mechanisms are disruptive and negative frequency-dependent forms of selection
45 (Oliviera et al. 2008; Hughes et al. 2013), both of which have been documented in theoretical,
46 laboratory, and field studies (Gross 1985, 1991, 1996; Oliviera et al. 2008). These forms of
47 selection are particularly important in the maintenance of polymorphism because negative
48 frequency dependence and disruptive selection are themselves variable forms of selection, the
49 former varying over space and time, the latter varying over the statistical distribution of
50 phenotypes.

51 Variable selection can also occur within a population when a trait that is expressed in both
52 males and females has alternative sex-specific fitness optima, resulting in sexually antagonistic
53 selection on that trait (Lande 1980). If that trait also has a common genetic basis in males and
54 females, then sexually antagonistic selection will lead to intralocus sexual conflict
55 (Bonduriansky and Chenoweth 2009). While others have proposed that intralocus sexual conflict
56 may maintain additive genetic variance (Rice and Chippindale 2001; Foerster et al. 2007) and
57 genetic polymorphism (Connallon and Clark 2012), result in balancing selection (Connallon and

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58 Clark 2014), and promote speciation (Bonduriansky 2011), the potential for intralocus sexual
59 conflict to maintain alternative reproductive tactics is comparatively understudied. There is
60 nevertheless reason to think that intralocus sexual conflict could be a potent force that maintains
61 variation in nature. Indeed, a growing body of evidence shows that selection on male ARTs and
62 the traits that differentiate them results in correlated evolution in females: genetic linkage
63 between male ARTs and female reproductive traits has been described in lizards (Sinervo and
64 Zamudio 2001), crickets (Heinen-Kay et al. 2020a; Richardson et al. 2021), and bulb mites
65 (Bielak et al. 2014; Buzatto et al. 2018; Buzatto and Clark 2020; Łukasiewicz et al. 2020).

66 While analytical models describe the action of selection on quantitative traits (Otto and Day
67 2007), correlated traits (Lande and Arnold 1983), and threshold traits including ARTs (Gross and
68 Repka 1998), we are unaware of any theory that simultaneously investigates evolution under
69 both sexually antagonistic selection on continuous quantitative traits and variable intersexual
70 genetic correlations. Here we take new steps towards understanding the role that intralocus
71 sexual conflict may play in the maintenance of sex-specific ARTs. We use a genetically explicit
72 individual-based model in which body size influences both female fecundity and male tactic
73 through a shared genetic architecture. By modeling ART maintenance under varying selection
74 regimes and levels of sex-specific gene expression, we explore the conditions under which
75 intralocus sexual conflict can maintain a hypothetical ART defined by larger (α) and smaller
76 (β) tactics.

77 To evaluate the potential for sexually antagonistic selection and intralocus sexual conflict to
78 maintain ARTs, we allowed a theoretical population to evolve under a range of scenarios
79 representing three different selection regimes acting on males: no selection, directional selection
80 against α males, and negative frequency-dependent selection. Within each selection regime

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81 we also varied the degree to which males and females could evolve independently by varying the
82 number of genetic loci with sex-dependent expression. We used these models to test our
83 hypothesis that intralocus sexual conflict may influence ART frequency over time, and that this
84 process might be altered by different selection regimes and/or the breakdown of intersexual
85 genetic correlations through sex-specific gene expression. Specifically, we predicted ARTs could
86 be maintained: (1) when alpha and beta males have equal probabilities of survival and mating but
87 intersexual heritability is low such that larger females do not necessarily produce larger (alpha)
88 sons, and (2) when alpha males are selected against but intersexual heritability of body size is
89 high such that low-fitness alpha males produce high-fitness daughters. While it is often assumed
90 that a male tactic that is larger, more sexually dimorphic, or that has sexually selected weapons
91 should have higher fitness, this need not necessarily be the case. Sexually-selected weapons
92 developed in fighter males are often costly to produce, requiring higher energy investment and
93 delayed development, both of which may contribute to higher mortality risk (Hunt and Simmons
94 1997). Fighter males often have higher testosterone levels than other male tactics, which can lead
95 to decreased survival (Sinervo et al. 2000a). In other cases, smaller males may have higher
96 fitness if shorter times to reach sexual maturity reduce their probability of mortality prior to
97 reproduction (Gross 1996).

98

99 **Methods**

100 Overview

101 In modeling the frequency of two different male ARTs – a larger “alpha” and smaller “beta”
102 male – we assumed that ART was a quantitative threshold trait determined by body size, which
103 in turn was entirely genetically controlled by 20 quantitative loci. Individual males with a body

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104 size greater than or equal to a threshold value became alpha males, and those below the threshold
105 became beta males. Females, which did not express these ARTs, had a fecundity value
106 proportional to their body size. For simplicity we assumed a discrete population of semelparous
107 individuals with non-overlapping generations. We did not include linkage disequilibrium or
108 mutations in our model; all genetic variance stemmed from an initial random draw of allele
109 values in the first generation.

110 To test our hypothesis that intralocus sexual conflict can affect the maintenance of ARTs, we
111 varied both the form of selection acting on the male ARTs and the intersexual heritability for
112 body size. We varied the form of selection on males by changing the relative fitness of each
113 tactic. We exposed the population to a null selection regime in which both male ARTs were
114 equally likely to survive and mate. We simulated sexually antagonistic selection by assigning
115 lower fitness to alpha males but higher fitness (fecundity) to larger females. Finally, we explored
116 the role of negative frequency-dependent selection in which the rare male ART in each
117 generation had a fitness advantage.

118 We altered the intersexual heritability of body size by varying the number of body size loci
119 that were “general” or “sex-specific” in their expression. When all 20 loci were “general,” the
120 effect of each allele controlling body size was the same in both sexes. This made size equally
121 heritable within and between the sexes, so larger (alpha) males produced larger (more fecund)
122 daughters than beta males. We predicted that correlated selection acting on males because of
123 fecundity selection might allow alpha males to persist in the population, even when directional
124 selection acts against them. However, as more loci become “sex-specific” – that is, allelic
125 expression depended on sex and genetic architecture for size was less shared between the sexes –
126 intersexual heritability should decline, and sire tactic should no longer influences daughter

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127 fitness. Thus, alpha males should no longer produce fitter daughters, and we predicted that
128 consistent directional selection against alpha males could result in their decline or disappearance
129 from the population.

130

131 The Model

132 We initiated each simulation with a parent generation comprised of 1000 diploid sexually
133 reproducing individuals (50:50 sex ratio). Each individual in our model had two traits that made
134 up its phenotype: sex and size. Sex was assigned randomly, and size was a quantitative trait
135 determined by the sum of allele values measured across 20 loci. To allow for sex-specific allelic
136 effects, each allele had two possible values (f and m) that influence body size. That is, each locus
137 had a total of three possible values that contribute to body size, and which value was expressed
138 depends on whether the locus was sex-specific or general and if the former, whether the
139 individual was male or female. For each sex-specific locus, only the two allele values
140 corresponding to that individual's assigned sex contributed to the body size value. This is the
141 biological equivalent of an allele that has sex-specific expression (Rice and Chippindale 2001).
142 For general loci the value of each allele at that locus was determined by averaging the allele's
143 two possible values. Allele values for the parent generation were drawn randomly from a normal
144 distribution with mean = 0 and SD = 0.5. We calculated the size of the individual from the
145 genotype using the following sex-specific equations:

$$146 \quad \text{Female Size} = \sum_{i=1}^{20-n} \frac{(f_{iD} + m_{iD})}{2} + \frac{(f_{iS} + m_{iS})}{2} + \sum_{i=20-n}^{20} f_{iD} + f_{iS} + C$$

$$147 \quad \text{Male Size} = \sum_{i=1}^{20-n} \frac{(f_{iD} + m_{iD})}{2} + \frac{(f_{iS} + m_{iS})}{2} + \sum_{i=20-n}^{20} m_{iD} + m_{iS} + C$$

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148 where n was the number of sex-specific loci, f and m are the female- and male-specific values,
149 respectively, of the two alleles at the i th locus inherited from the dam (D subscript) or the sire (S
150 subscript), and C is a constant. The first summation calculated the component of the phenotypic
151 value contributed from the general loci; the second summation calculated the contribution of the
152 sex-specific loci. Adding a constant to the expression ensured that size remained a positive
153 number with a mean of C in the parent generation; any individual whose calculated size was less
154 than zero was assigned a size of zero. We arbitrarily set $C = 10$ for our simulations.

155 Male mating tactic was determined by threshold body size: males with size greater than or
156 equal to 10 were alpha males and those with size less than 10 were beta males. Fecundity was
157 assigned to females as a function of size:

$$158 \quad \text{Fecundity} = \frac{12 \times \text{size}^2}{\text{size}^2 + 100}$$

159 such that fecundity increased asymptotically with increasing body size to a maximum value
160 approaching 12 offspring at a size of 40. This set an upper limit on fecundity selection while
161 preserving positive directional selection on female size.

162 We modeled the evolution of male and female body size and ART frequency under seven
163 different selection regimes on male body size and five different values for the number of sex-
164 specific loci for a total of 35 different model scenarios (Table 1). These varied in the degree to
165 which selection on size was sexually antagonistic and in the intersexual heritability of size, thus
166 creating a spectrum of intralocus sexual conflict. We varied direct selection on males by
167 changing the relative combined probability of survival and mating (hereafter W_T for each tactic).
168 In the “no selection” model individuals of both ARTs had equal values of W . In three separate
169 “directional selection” models we set $W_a = 1$ and $W_b = 1.5, 1.8, \text{ or } 2$. This allowed us to evaluate
170 how the strength of direct selection on male tactic affected ART maintenance in the face of

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171 intralocus sexual conflict. In each directional selection model, W_a and W_b were held constant
172 across generations. In three separate “negative frequency-dependent selection” models, each
173 tactic’s W varied as function of its frequency (F_T) such that the rare tactic in each generation
174 always had a higher mating probability ($1 - F_T$). We ran three different negative frequency-
175 dependent models which ranged in starting frequency ratios of alpha and beta males from $F_a:F_b$
176 = 2:1, 1:1, and 1:2. This allowed us to evaluate how initial tactic frequencies affected ART
177 maintenance under negative frequency-dependent selection.

178

179 **Table 1.** Parameters and values modeled, resulting in 35 total scenarios modeled. Each scenario
180 varied in the form of selection on males and the number of sex-specific loci. Negative frequency
181 dependent models also varied in the starting frequency ratio of alpha to beta males ($F_a:F_b$);
182 directional selection models also varied in the ratio of alpha fitness to beta fitness ($W_a:W_b$).

Parameter	Values modeled
Selection Regime	No Selection, $W_a = W_b$
	Negative frequency dependent selection, $F_a:F_b = 1:1$
	Negative frequency dependent selection, $F_a:F_b = 1:2$
	Negative frequency dependent selection, $F_a:F_b = 2:1$
	Directional selection against alphas, $W_a:W_b = 1:1.5$
	Directional selection against alphas $W_a:W_b = 1:1.8$
	Directional selection against alphas $W_a:W_b = 1:2$
# Sex-Specific Loci	0, 5, 10, 15, 20

183

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184 In all models, W_f did not differ among individual females, but the proportion of females that
185 survived to mate in each generation declined with population size to simulate density-dependent
186 population growth regulation. The proportion of females surviving to mate (M_f) was calculated
187 anew for each generation using the equation:

$$188 \quad M_f = \frac{0.5}{1 + e^{-2+KN}}$$

189 where K is a constant and N is the current population size. We chose $K = 0.0015$ such that this
190 equation defined a sigmoidal curve that decreased from 0.44 at $N = 0$ to 0.04 at $N = 3000$. For
191 each generation the number of females that were allowed to reproduce (D) was calculated as:

$$192 \quad D = M_f N$$

193 D females were randomly chosen to be dams. D males were similarly chosen to be sires but
194 sire selection was weighted by W_T . Dams were randomly paired with sires (no assortative
195 mating), and a number of offspring equivalent to the dam's fecundity were created. Each
196 offspring inherited alleles at all 20 loci in a Mendelian fashion such that at each locus the
197 offspring inherits one allele from the dam and one from the sire, and the allele inherited from
198 each parent is randomly drawn from the two alleles each parent possesses. Sex was assigned
199 randomly to offspring to achieve an approximately equal sex ratio, and size, fecundity, and
200 mating probability were calculated for each offspring as described above for individuals in the
201 parent generation. These offspring were then used as parents for the next generation, and the
202 model was iterated for a total of 500 generations in each model scenario. We ran 11 replicates of
203 the full set of the 35 model scenarios to ensure that results did not qualitatively differ among
204 model runs.

205

206 Analysis

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207 In each of the 35 model scenarios, for each generation we calculated (1) intra- and
208 intersexual heritability of size (to understand the degree to which males and females could
209 respond independently to selection), (2) the sex-specific mean and variance of size (to
210 understand the degree of sexual dimorphism that evolved and the opportunity for selection), (3)
211 sex-specific selection gradients for size (to understand the degree to which selection was
212 sexually antagonistic), and (4) the frequency of ARTs (to understand how intralocus sexual
213 conflict affects ART maintenance). Intra- and intersexual heritabilities were calculated by
214 doubling the regression coefficient of the sex-specific mean offspring size regressed on sex-
215 specific parent size (Falconer and Mackay 1960). Sex-specific selection gradients for each
216 generation were calculated as the slope of the regression of relative fitness on standardized body
217 size. Relative fitness for each sex was calculated by dividing the number of offspring produced
218 by each individual by the mean number of offspring produced by that sex; standardized body
219 size was calculated by scaling each individual's body size to the sex-specific mean and dividing
220 by the sex-specific standard deviation. We then recorded how each of these factors changed
221 across generations (i.e., as additive genetic and phenotypic variance change), and how that
222 change varied with (1) the selection regime and (2) the number of loci that were sex-specific
223 rather than general in their effect on body size. Finally, given that intralocus sexual conflict is
224 known to affect intrinsic population growth rates, we also plotted population size over 500
225 generations for each selection regime and calculated geometric mean population growth rates
226 (Lewontin and Cohen 1969) for each selection regime and number of sex-specific loci. Using
227 data from all 11 replicates of each of the 35 model scenarios, we used linear models to determine
228 whether geometric mean population growth rates differed with the number of sex-specific loci in
229 each selection regime.

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230

231 Results

232 Results were not qualitatively different among the 11 replicate sets of model runs. Therefore,
233 for all analyses except population growth rates, we report results from a single set of 35 model
234 runs.

235 Increasing the number of sex-specific loci decreased intersexual heritability. Intrasexual
236 heritability was approximately 1 and was constant across selection regimes, numbers of sex-
237 specific loci, and generations. Intersexual heritability generally decreased from 1 to 0 as the
238 number of sex-specific loci increased from 0 to 20 (Figure 1). This trend was consistent across
239 all selection regimes.

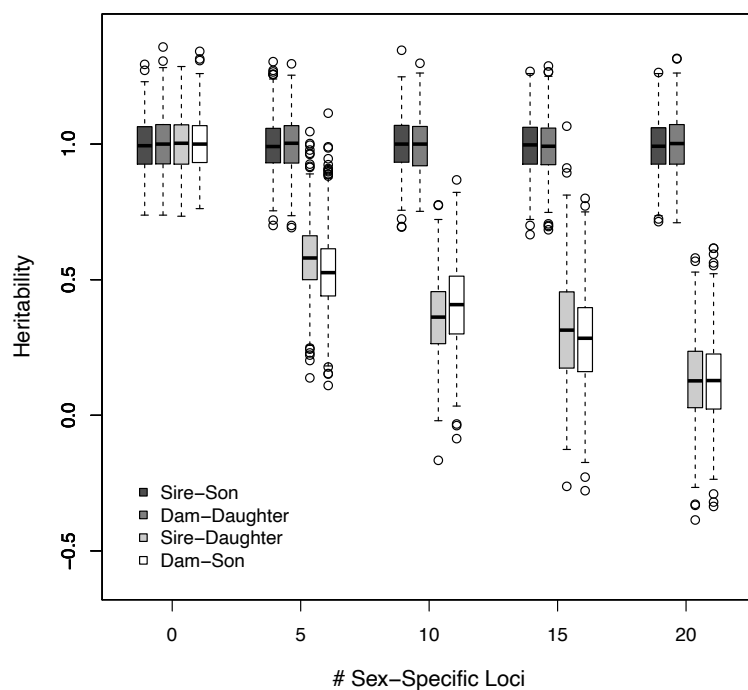


Figure 1. Box plots show mean values of inter- and intrasexual heritability averaged across 500 generations in a “no selection” simulation. Intersexual heritability declined as the number of sex-specific loci increased. Intrasexual heritability for body size did not vary with the number of sex-specific loci. Results were qualitatively similar across all other selection regimes.

240

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241 Increasing the number of sex-specific loci also facilitated the evolution of sexual size
242 dimorphism. Sexual dimorphism evolved in all selection regimes when intersexual heritability
243 was less than 1 (>0 sex-specific loci; Figure 2). The rate and degree to which the sexes diverged
244 in body size depended on the selection regime and the number of sex-specific loci (i.e., the
245 intersexual heritability). In all cases, sexual dimorphism evolved faster and to a greater degree
246 when intersexual heritability was low (fewer sex-specific loci) and when selection was sexually
247 antagonistic (males experienced directional selection favoring betas). This result is consistent
248 with existing literature and theory on the evolution of sexual dimorphism (Cox and Calsbeek
249 2009).

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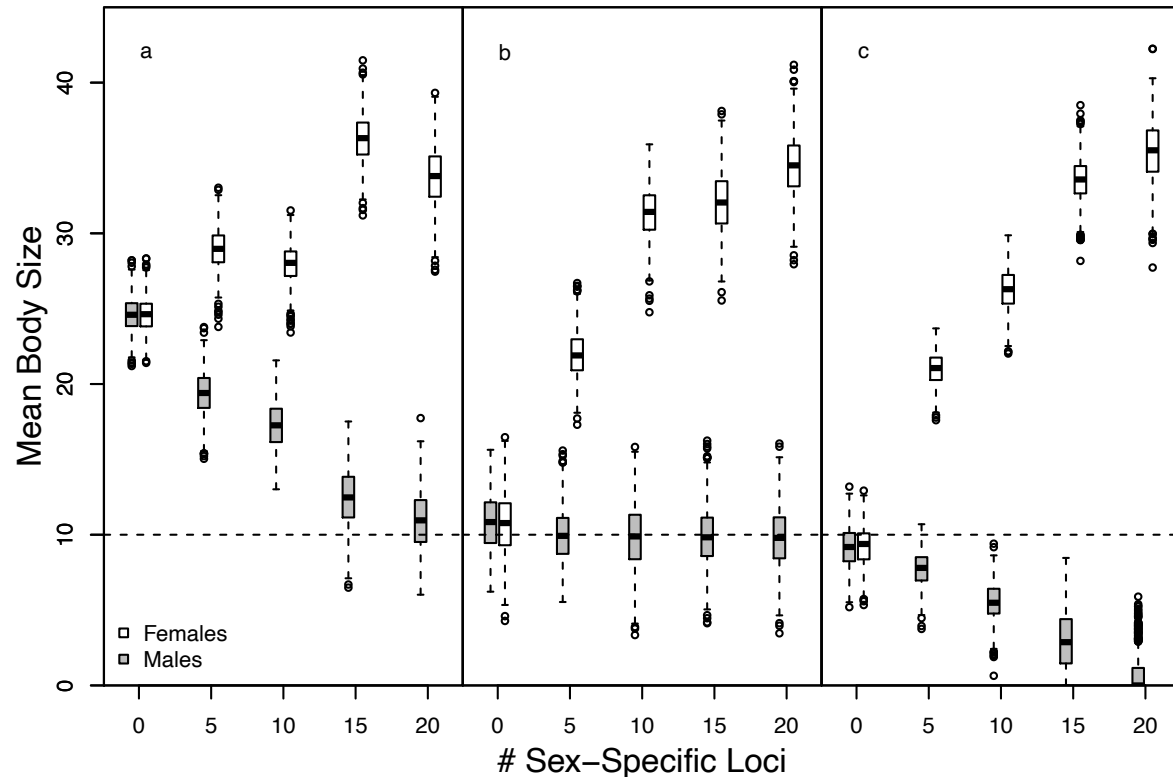


Figure 2. Boxplots showing the final mean body size of females and males across a range of the number of sex-specific loci and three different selection regimes in (a) a no selection regime, (b) a negative frequency-dependent selection regime in which initial tactic frequencies were equal, and (c) a directional selection regime in which beta males were 1.8 x more likely to survive and mate than alpha males. Dotted horizontal line represents the size threshold separating alpha and beta males, therefore male boxplots overlapping this line indicate that both tactics persisted over 500 generations in that scenario. Results from negative frequency-dependent selection regimes with different initial frequencies and from directional selection regimes with different mating probability ratios are qualitatively the same as (b) and (c), respectively, and are not shown here.

250

251 Sex-specific selection gradients reflected the imposed selection regimes initially in all
252 selection regimes (Figure 3). In subsequent generations, selection gradients for both males and
253 females converged on zero in most models, as the population responded to selection and body
254 size evolved. Smaller selection gradients in later generations reflected a reduction in the variance
255 in male body size (as body size responds to selection), a reduction in the covariance between
256 female body size and fecundity (as females reach a size at which the fecundity-body size
257 relationship asymptotes), or both. Differences in sex-specific selection gradients were maintained
258 in the directional and negative frequency-dependent selection regimes in which intersexual

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259 heritability was high (zero sex-specific loci) and ARTs were maintained.

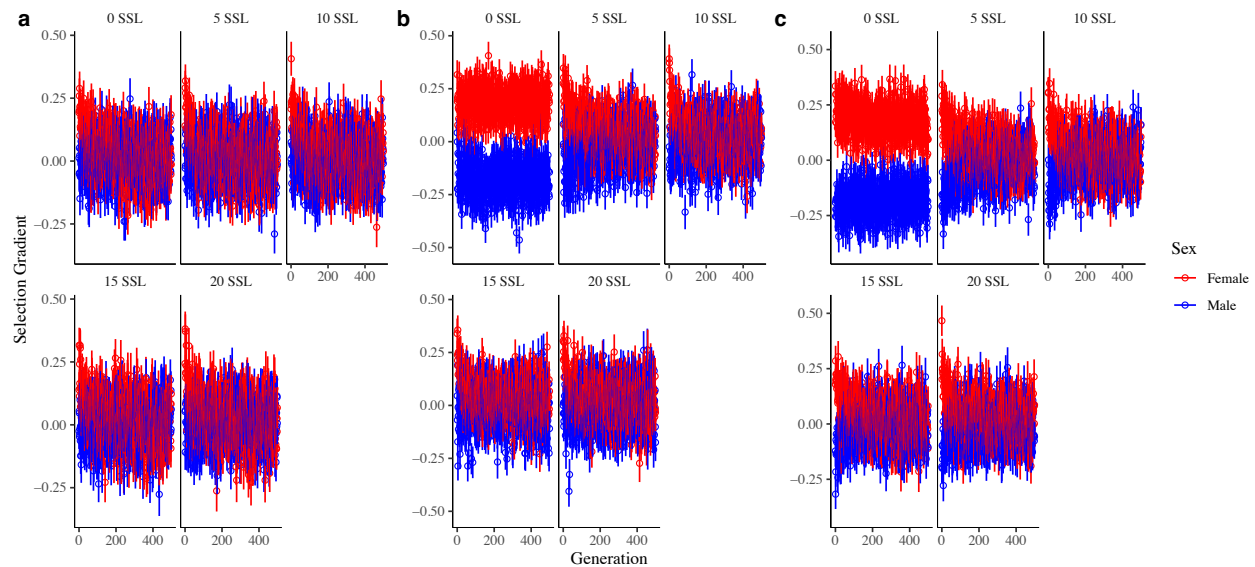


Figure 3. Selection gradients on males and females over 500 generations and across a range of the number of sex-specific loci (nSSML) in (a) a no selection regime, (b) a negative frequency-dependent selection regime in which initial tactic frequencies were equal ($F_a=F_b$), and (c) a directional selection regime in which beta males were 1.8 x more likely to survive and mate than alpha males. Differences in sex-specific selection gradients were maintained in (b) the negative frequency-dependent and (c) directional selection regimes in which intersexual heritability is high (zero sex-specific loci), constraining the evolution of sexual dimorphism and maintaining the gender load.

260

261 Selection regimes and intersexual heritabilities affected geometric mean population growth
262 rates ($F_{7,377} = 23.91, p \ll 0.0001$). In most models, population size increased from 1000 in the
263 parent generation to an asymptote of approximately 2000 individuals (Figure 4). However, in all
264 the directional selection and negative frequency-dependent selection regimes, population size
265 and geometric mean population growth rate were greatly reduced when there were zero sex-
266 specific loci (i.e., when intersexual heritabilities were approximately 1). In no-selection regimes,
267 geometric mean population growth rates did not differ across numbers of sex-specific loci (mean
268 \pm SD = $0.0038 \pm 0.00038, F_{1,53} = 0.038, p > 0.8$). In negative frequency-dependent and
269 directional selection regimes, geometric mean population growth rates differed across numbers
270 of sex-specific loci (negative frequency-dependent selection: $F_{1,163} = 111.19, p \ll 0.0001$;
271 directional selection: $F_{1,163} = 56.39, p \ll 0.0001$) such that they were lowest when the number of

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272 sex-specific loci was zero. The degree to which population growth rate was reduced when there
273 were no sex-specific loci (compared to other values of sex-specific loci) did not vary with
274 different starting frequencies in the negative frequency-dependent selection models ($F_{2,30} = 2.21$,
275 $p = 0.13$). However, in directional selection regimes with zero sex-specific loci (i.e. models with
276 intralocus sexual conflict), population growth rates decreased as the strength of directional
277 selection against large (alpha) males increased ($F_{2,30} = 45.65$, $p \ll 0.0001$). These reductions in
278 population size and geometric mean population growth rate were consistent with the unresolved
279 gender load maintained when males and females were not able to evolve independently
280 (Arnqvist and Tuda 2010). The maintenance of the gender load over time was evident in the sex-
281 specific selection gradients for the directional selection simulations with no sex-specific loci
282 (Figure 3).

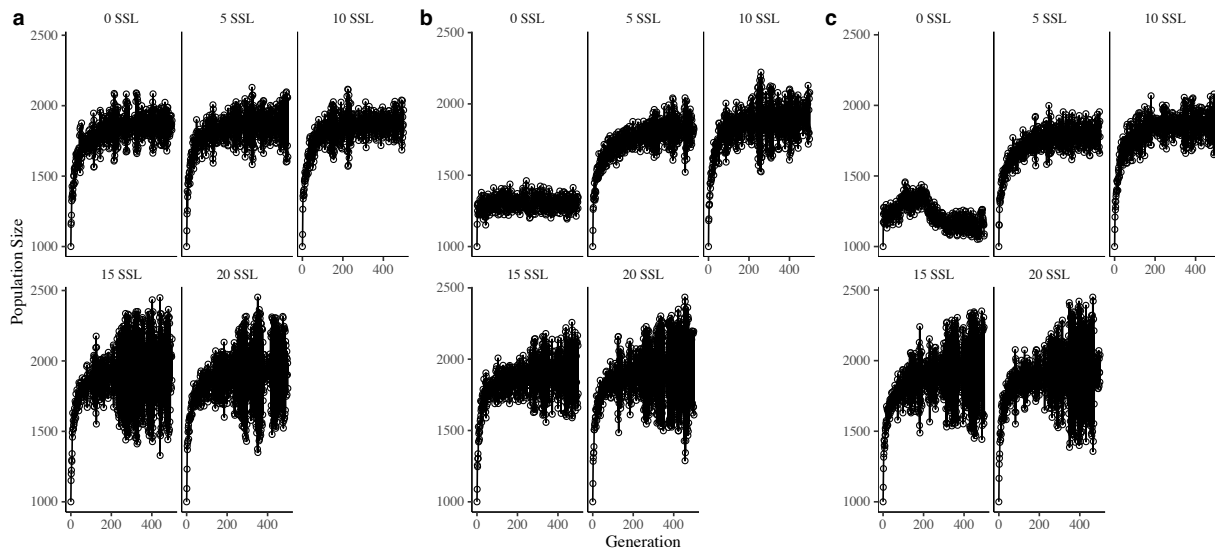


Figure 4. Population sizes over 500 generations and across a range of the number of sex-specific loci (nSSML) in (a) a no selection regime, (b) a negative frequency-dependent selection regime in which initial tactic frequencies were equal ($F_a = F_b$), and (c) a directional selection regime in which beta males were 1.8 x more likely to survive and mate than alpha males. In (b) the negative frequency-dependent and (c) directional selection regimes in which intersexual heritability is high (zero sex-specific loci), population size is reduced because of the gender load.

283

284 Alternative reproductive tactics were maintained under three different conditions, comprising

285 19 of the 35 total scenarios we modeled. Of the 19 scenarios in which ARTs were maintained, 15

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286 were under negative frequency-dependent selection, 2 were under the no selection regime, and 2
287 were under the directional selection regime. First, under negative frequency-dependent selection
288 (i.e., the probability of mating for tactic T is $1-F_T$), both tactics were maintained regardless of
289 initial tactic frequencies or the degree of intersexual heritability (Figure 5). This result was
290 consistent across all 11 replicate model runs.

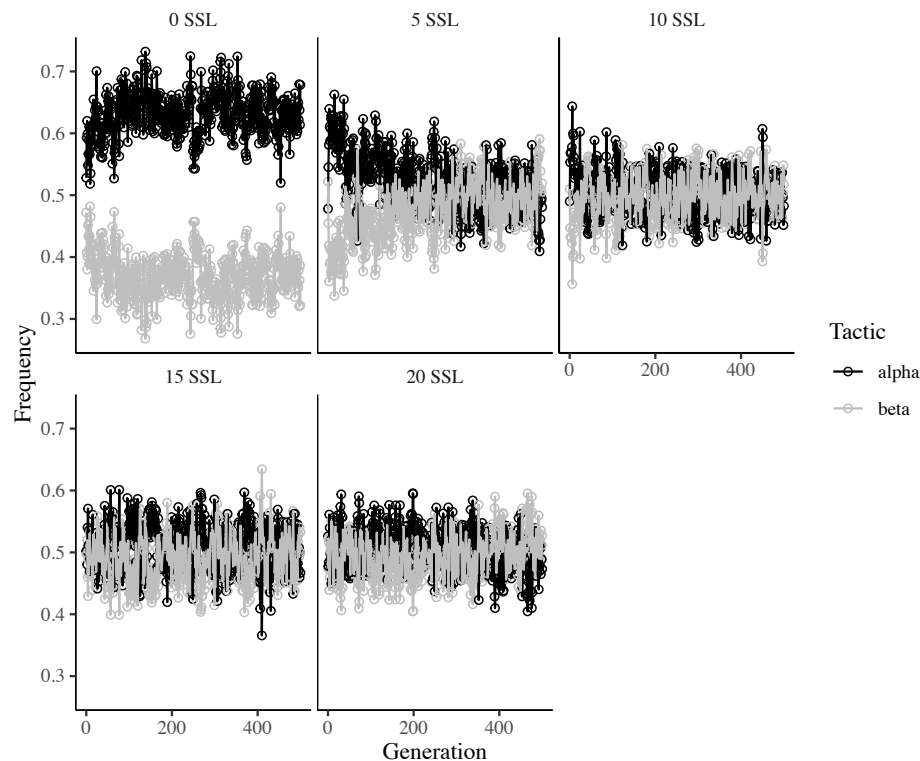


Figure 5. Frequency of alpha and beta males over 500 generations and across a range of the number of sex-specific loci (nSSML) in a “frequency-dependent selection” regime in which initial tactic frequencies were equal ($F_a=F_b$). Tactic frequencies were not qualitatively different when initial tactic frequency ratios were 2:1 or 1:2 and are thus not shown here.

291

292 There are two general situations besides negative frequency-dependent selection, comprising
293 4 modeled scenarios, in which ARTs were preserved across 500 generations in our model. First,
294 ARTs were maintained in the no selection regime when intersexual heritability was low (e.g., 15
295 or 20 sex-specific loci; Figure 6). Under no selection and 15 sex-specific loci, both tactics
296 persisted over 500 generations in 9 of 11 model runs; under no selection and 20 sex-specific loci,

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297 both tactics persisted over 500 generations in 10 of 11 model runs. In these same models, alpha
298 males comprised >75% of the population by the 500th generation in 10 out of 11 “no selection”
299 model runs with 15 sex-specific loci and 5 out of 11 “no selection” model runs with 20 sex-
300 specific loci. Across all 11 “no selection” model run replicates, increasing the number of sex-
301 specific loci resulted in a slower trend toward fixation of alpha males (Figure 6).

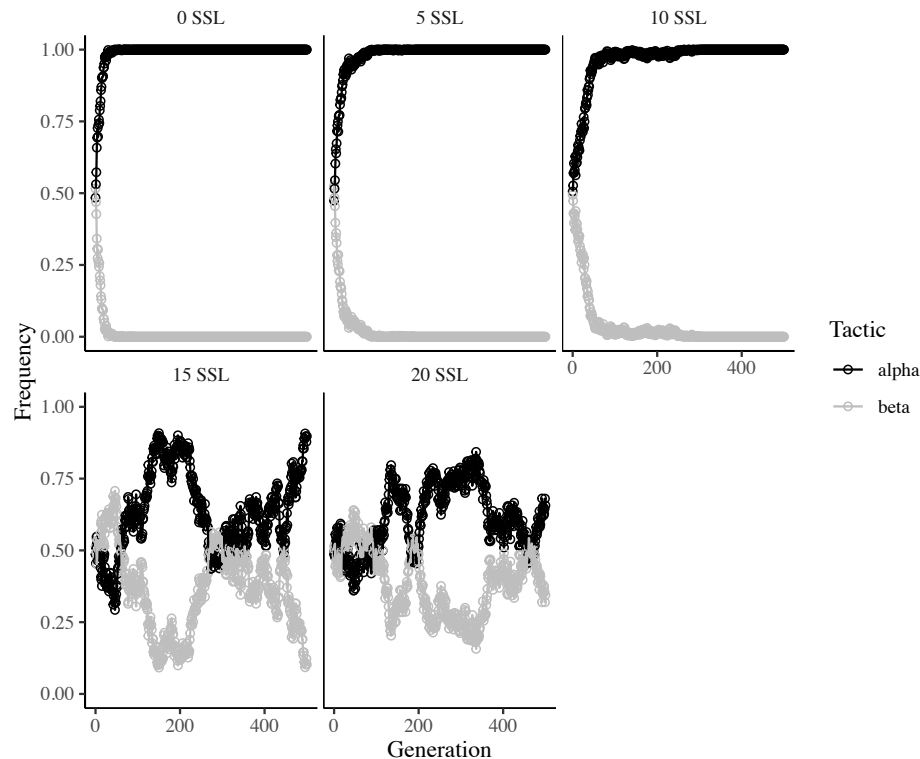


Figure 6. Frequency of alpha and beta males over 500 generations and across a range of the number of sex-specific loci (nSSML) in a “no selection” regime.

302

303 ARTs were also maintained by intralocus sexual conflict over body size. This occurred when
304 selection on size was sexually antagonistic (favoring small males and large females) and
305 intersexual heritability was high (e.g., zero sex-specific loci / all loci affect males and females
306 equally; Figure 7). This was especially evident at intermediate strengths of directional selection
307 (e.g., when beta males were 1.8 – 2 times more likely to survive and reproduce than alpha
308 males), where direct selection on males was strong enough to reduce the frequency of alphas but

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309 weak enough not to eliminate them entirely. In this situation ARTs were maintained because
310 there was a balance between (a) correlated fecundity selection and high intersexual heritability
311 producing larger sons and (b) selection against those large sons. This outcome was consistent
312 across all 11 replicates of our model runs.

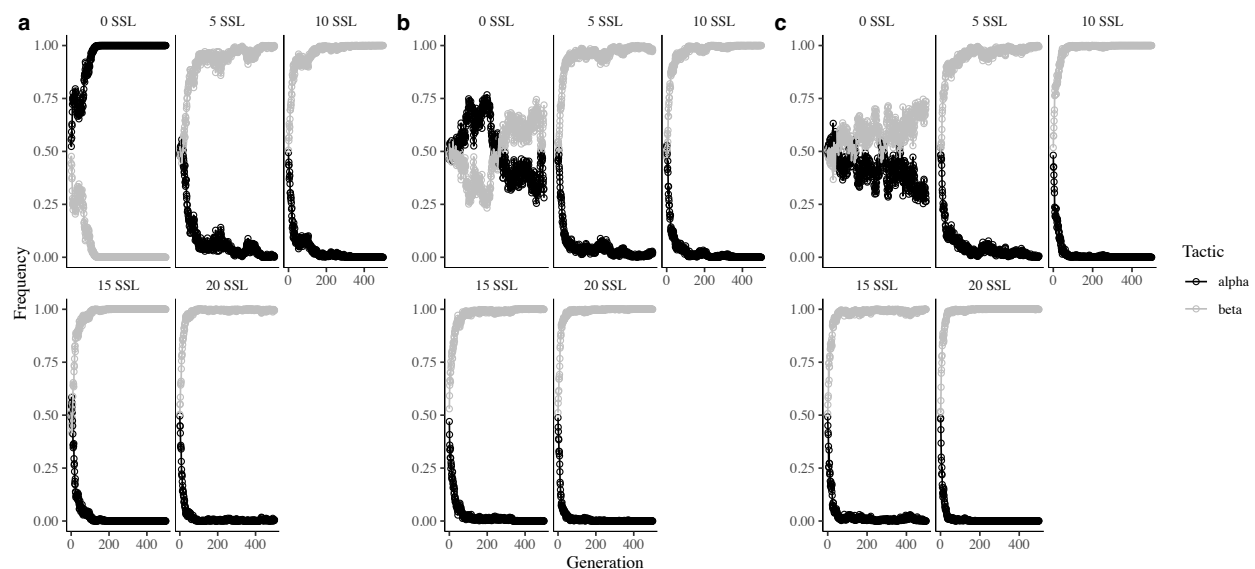


Figure 7. Frequency of alpha and beta males over 500 generations and across a range of the number of sex-specific loci in a “directional selection” regime in which the mating probability of beta males was (a) 1.5, (b) 1.8, and (c) 2 times that of alpha males.

313

314

315 Discussion

316 Alternative reproductive tactics abound in nature (Sinervo and Calsbeek 2010), yet few
317 processes have been identified that sustain them. Those that have been identified – negative
318 frequency-dependent selection and disruptive selection – both focus on selection acting directly
319 on the sex exhibiting the polymorphism (Sinervo and Calsbeek 2006). We show that selection
320 acting on both sexes, and intralocus sexual conflict that results when genetic architecture is
321 shared, may also preserve sex-specific alternative reproductive tactics over hundreds of
322 generations. If male ARTs differentially affect the fitness of their daughters, then they can be

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323 maintained (or eliminated) by selection for (against) their daughters even in the absence of
324 negative frequency-dependent fitness.

325 In addition to negative frequency-dependent selection, two other processes emerged from our
326 model that preserved alternative tactics over 500 generations. First, both tactics persisted when
327 there was no direct selection on males, and most (15) or all (20) loci were sex-specific in their
328 expression. In this scenario there was also no correlated selection on males, because males could
329 not pass on their size to their daughters. Fecundity selection favored large females, but these
330 females could not pass on their large size to their sons because intersexual heritability was zero.
331 Thus, there was neither direct nor correlated selection on male size, allowing the persistence of
332 both tactics over 500 generations. The fact that alpha males comprised the majority of males by
333 the 500th generation in most of these model runs suggests that these scenarios could not maintain
334 ARTs indefinitely. However, because the trend toward an alpha male majority occurred more
335 slowly in these models as the number of sex-specific loci increased, low intersexual heritability
336 could play a role in preserving male ARTs in natural populations where selection on males is
337 chronically weak or temporally and spatially variable.

338 The second scenario in which both ARTs were maintained over 500 generations was when
339 beta males were 1.8 – 2 times more likely to survive and mate than alpha males, and the number
340 of sex-specific loci was zero. This created a scenario in which males experienced direct selection
341 favoring beta males and correlated selection favoring alpha males. Because no loci were sex-
342 specific in their expression, size was heritable between the sexes, creating intralocus sexual
343 conflict. When the strength of directional selection on male size was low (i.e., the fitness of betas
344 was just 1.5 times higher than that of alphas), correlated selection outweighed direct selection
345 and alpha males went to fixation. However, as the strength of directional selection increased,

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346 direct and correlated selection balanced each other out, and both tactics persisted over 500
347 generations.

348 Persistent intralocus sexual conflict in these scenarios was evident in the maintenance of the
349 gender load. Selection gradients on females remained positive and those on males remained
350 negative throughout these simulations due to intralocus sexual conflict constraining the evolution
351 of sexual dimorphism. In concordance with theory, the maintenance of the gender load in these
352 simulations resulted in a lower population growth rate compared with simulations in which the
353 sexes could respond independently to selection. This finding shows that the maintenance of
354 ARTs, when achieved through intralocus conflict, may reduce population fitness.

355 Our model also showed that one male tactic could go to fixation even when males did not
356 experience direct selection. When females were selected to be larger, but male body size did not
357 experience direct selection, alpha males became fixed in the population when intersexual
358 heritability for body size was high. This occurred through correlated fecundity selection. This
359 finding, though not explicitly predicted, again highlights the importance of understanding
360 selection in both sexes when attempting to understand the evolutionary maintenance of sex-
361 specific polymorphisms.

362 Our models consistently revealed that sexual conflict resulted in the persistence of a sex-
363 specific polymorphism over hundreds of generations, even in the absence of negative frequency-
364 dependent or disruptive selection. This result is consistent with a growing literature documenting
365 genetic correlations between male ARTs and female fitness, suggesting that the maintenance of
366 sex-specific ARTs through intralocus sexual conflict may be common and widespread in nature.
367 For example, side-blotched lizards (*Uta stansburiana*) exhibit three male morphs associated with
368 orange, blue, and yellow throat colors (Sinervo and Lively 1996). In this system the intersexual

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369 heritability of throat color is high, and female throat color is correlated with fecundity, such that
370 the genes associated with male ART have direct consequences for female fitness and population
371 growth rate (Sinervo and Zamudio 2001). Though negative frequency-dependent selection seems
372 partly responsible for ART maintenance in this system, genetic correlations between male tactic
373 and female fitness also have the potential to affect ART frequencies (Sinervo and Zamudio
374 2001).

375 Male Pacific field crickets (*Teleogryllus oceanicus*) in Hawaii exhibit singing and silent
376 reproductive tactics that stem from different wing morphologies (normal and flatwing; Zuk et al.
377 2006). These wing morphologies can be inherited and expressed by daughters, and flatwing
378 females invest less in reproductive tissue mass, experience more frequent mating failure, and are
379 less likely to mount and mate with males compared to normal females (Heinen Kay et al. 2019;
380 Heinen-Kay et al. 2020b; Richardson et al. 2021). Because flatwing males have much higher
381 survival (Zuk et al. 2006) and sire more offspring than normal males (Heinen-Kay et al. 2019),
382 while flatwing females seem to have lower fitness, intralocus sexual conflict over wing
383 morphology is likely driving the maintenance of both male ARTs (Heinen-Kay et al. 2020b).

384 Studies of the bulb mite (*Rhizoglyphus* spp.) are also consistent with ART maintenance
385 through intralocus sexual conflict. In artificial selection experiments, females from lines selected
386 for fighter males have lower fitness (fecundity and longevity) than females from lines selected
387 for sneakers (Bielak et al. 2014; Łukasiewicz et al. 2020). Harano et al. (2010) showed the same
388 pattern in flour beetles (*Gnatocerus cornutus*) using an artificial selection experiment in which
389 they selected for larger or smaller male mandibles. While flour beetles do not have ARTs *per se*,
390 they do exhibit sexual dimorphism in a sexually selected weapon, and the intralocus sexual

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391 conflict arising from simultaneous sexually antagonistic selection and an intersexual genetic
392 correlation for mandible size could maintain variation in males as shown in the present paper.

393 While the concepts of intralocus sexual conflict and correlated selection are decades old
394 (Lande and Arnold 1983; Rice and Chippindale 2001), they have only just begun to penetrate the
395 literature on alternative reproductive tactics. Our results show that intralocus sexual conflict can
396 play a role in the maintenance of ARTs, and that understanding the maintenance - or elimination
397 - of sex-specific polymorphisms requires considering selection in both sexes. Fruitful systems in
398 which to look for this phenomenon in nature will include those in which the trait or traits that
399 differentiate ARTs are also expressed in females (e.g., body size), or those in which genetic
400 correlations between ARTs and female survival or reproductive success have already been
401 established.

402

403 **Data Availability Statement:** The individual-based model used in this paper will be uploaded to
404 Dryad upon acceptance.

405

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