Title: Intralocus sexual conflict can maintain alternative reproductive tactics

Running Title: Sexual conflict maintains ARTs

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Abstract

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

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

Introduction

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

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

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

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

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

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

Methods

Overview

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

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

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

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

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

The Model

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

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

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

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

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

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

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

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

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

Table 1. Parameters and values modeled, resulting in 35 total scenarios modeled. Each scenario varied in the form of selection on males and the number of sex-specific loci. Negative frequency dependent models also varied in the starting frequency ratio of alpha to beta males (*Fa:Fb*); 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

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

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

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

$$D = M_f N$$

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

Analysis

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

Results

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

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

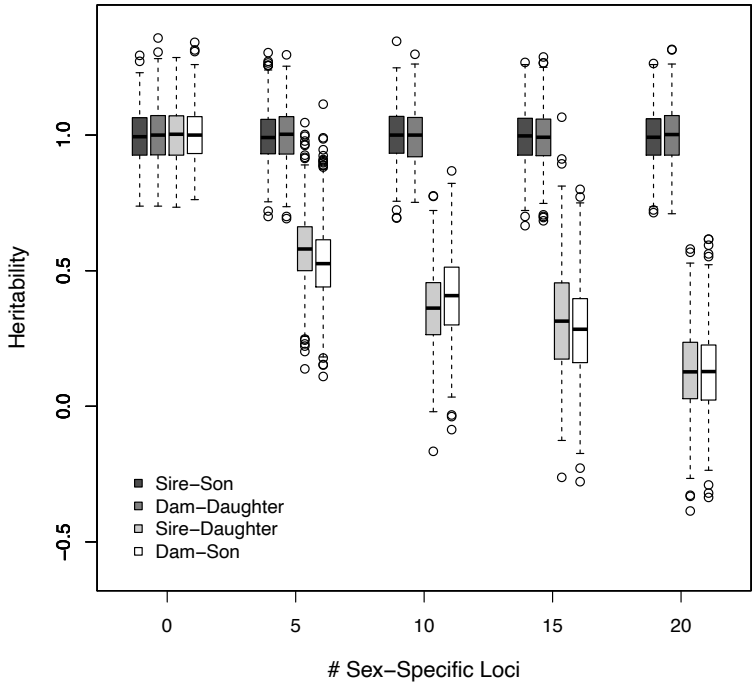

Figure 1. Box plots show mean values of inter- and intrasexual heritability averaged across 500 generations in a "no selection" simulation. Intersexual heritability declined as the number of sex-specific loci increased. Intrasexual heritability for body size did not vary with the number of sex-specific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

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

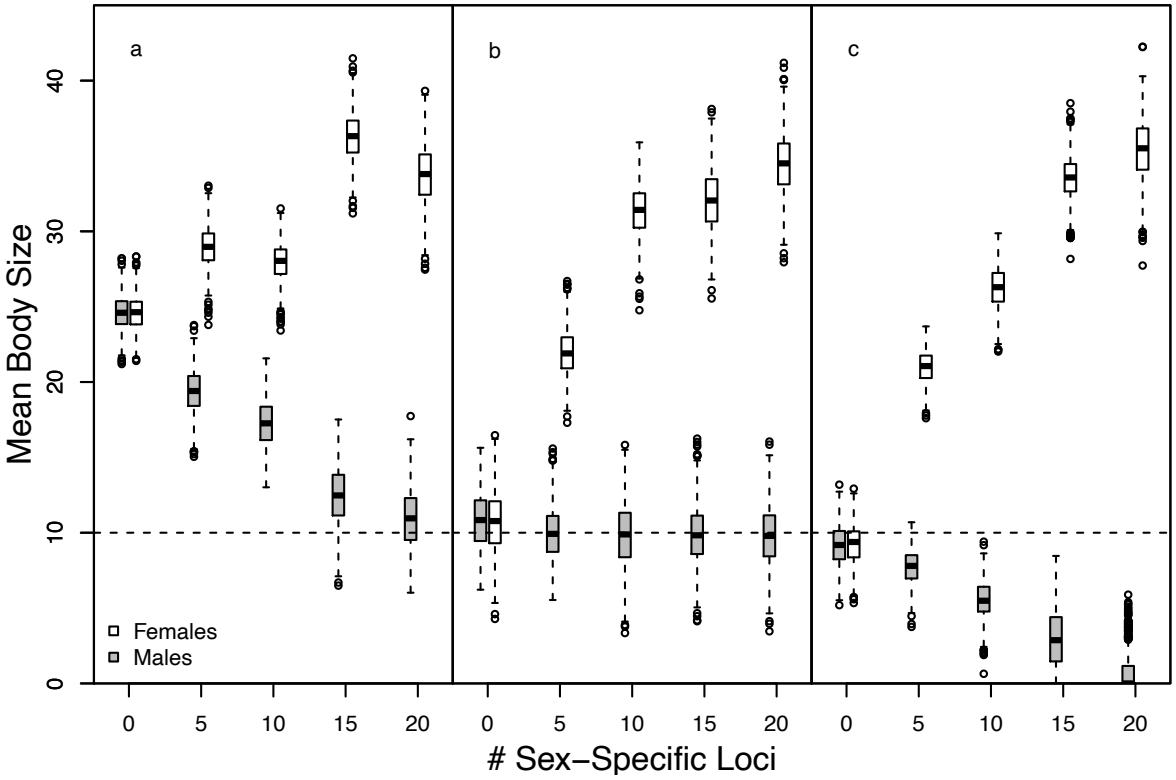

Figure 2. Boxplots showing the final mean body size of females and males across a range of the number of sex-specific loci and three different selection regimes in (a) a no selection regime, (b) a negative frequency-dependent selection regime in which initial tactic frequencies were equal, and (c) a 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.

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

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

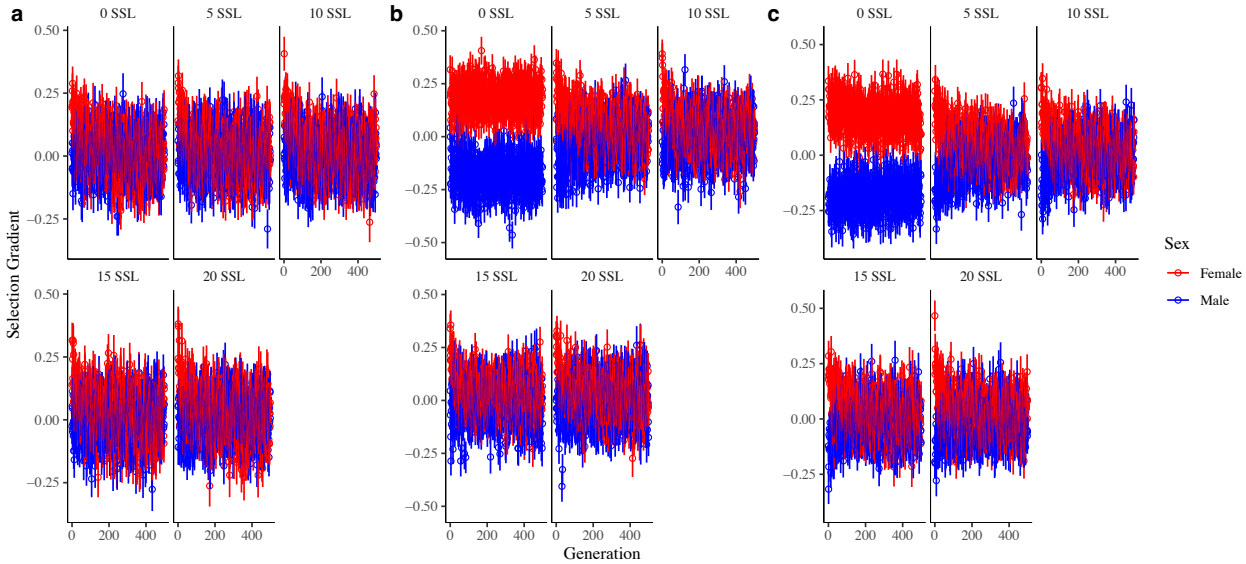

Figure 3. Selection gradients on males and females over 500 generations and across a range of the number of sex-specific loci (nSSML) in (a) a no selection regime, (b) a negative frequency-dependent selection regime in which initial tactic frequencies were equal (F_a=F_b), and (c) a directional selection 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.

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

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

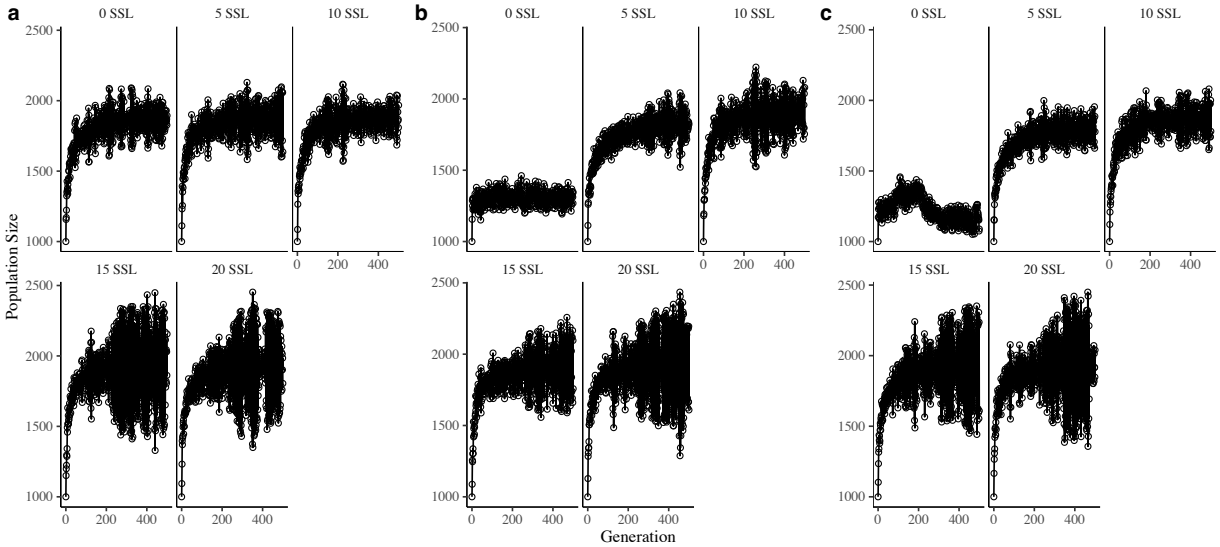

Figure 4. Population sizes over 500 generations and across a range of the number of sex-specific loci (nSSML) in (a) a no selection regime, (b) a negative frequency-dependent selection regime in which initial tactic frequencies were equal (F_a=F_b), and (c) a directional selection regime in which beta 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.

Alternative reproductive tactics were maintained under three different conditions, comprising 19 of the 35 total scenarios we modeled. Of the 19 scenarios in which ARTs were maintained, 15

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

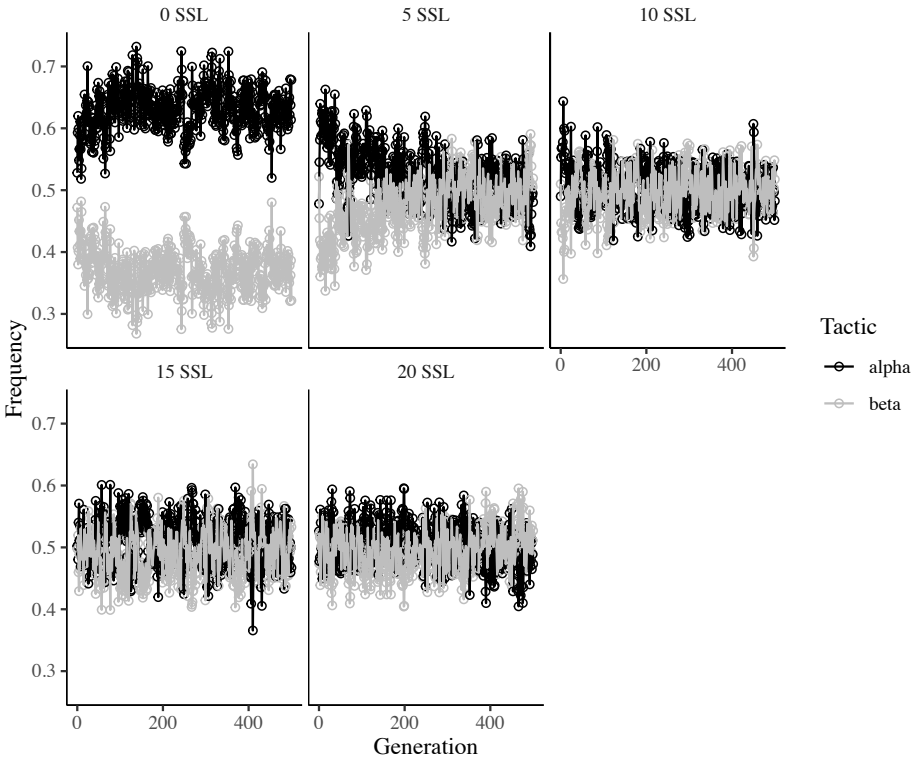

Figure 5. Frequency of alpha and beta males over 500 generations and across a range of the number of sex-specific loci (nSSML) in a "frequency-dependent selection" regime in which initial tactic frequencies were equal (F_a=F_b). Tactic frequencies were not qualitatively different when initial tactic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

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

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

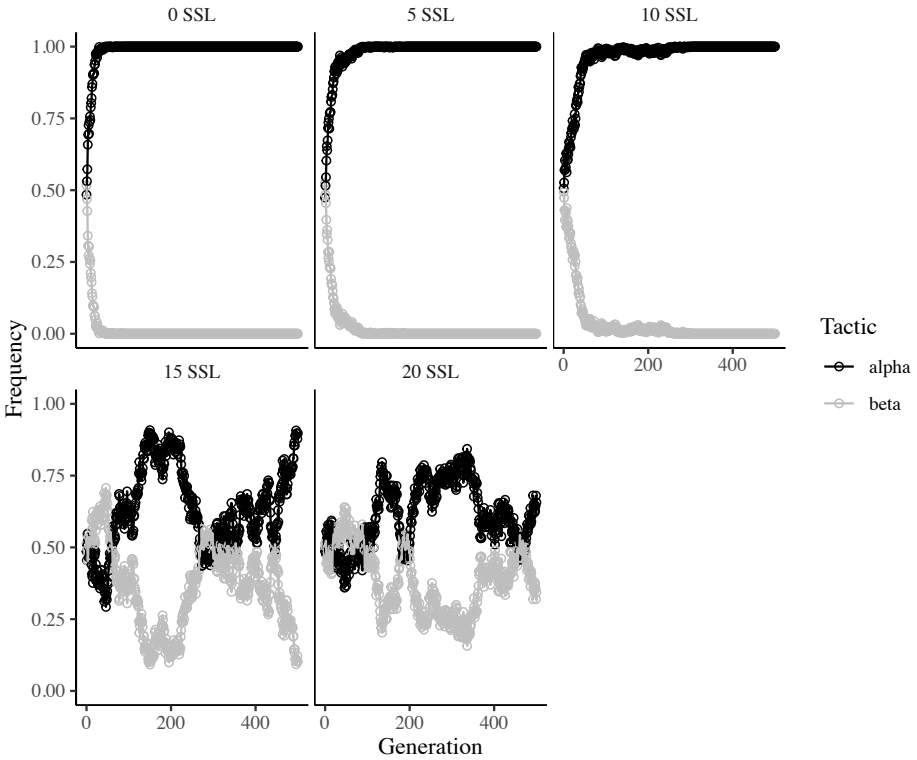

Figure 6. Frequency of alpha and beta males over 500 generations and across a range of the number of sex-specific loci (nSSML) in a "no selection" regime.

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

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

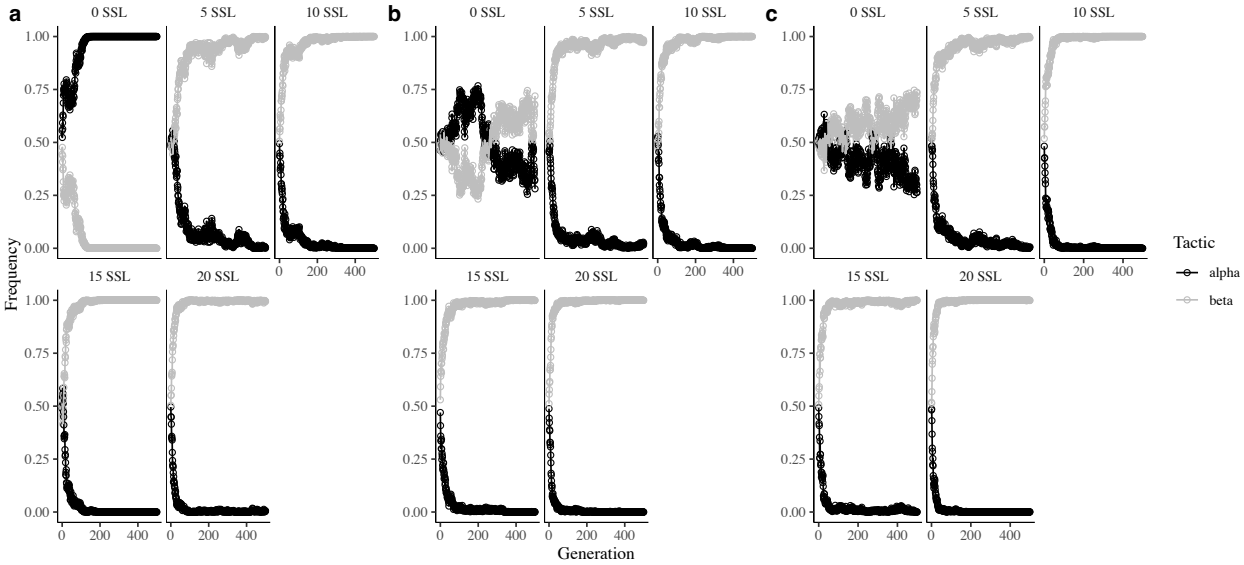

Figure 7. Frequency of alpha and beta males over 500 generations and across a range of the number of sex-specific loci in a "directional selection" regime in which the mating probability of beta males was (a) 1.5, (b) 1.8, and (c) 2 times that of alpha males.

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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