

Sexually Antagonistic Selection, Sexual Dimorphism, and the Resolution of Intralocus Sexual Conflict

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ABSTRACT: Males and females share most of their genomes and express many of the same traits, yet the sexes often have markedly different selective optima for these shared traits. This sexually antagonistic (SA) selection generates intralocus sexual conflict that is thought to be resolved through the evolution of sexual dimorphism. However, we currently know little about the prevalence of SA selection, the components of fitness that generate sexual antagonism, or the relationship between sexual dimorphism and current SA selection. We reviewed published studies to address these questions, using 424 selection estimates representing 89 traits from 34 species. Males and females often differed substantially in the direction and magnitude of selection on shared traits, although statistically significant SA selection was relatively uncommon. Sexual selection generated stronger sexual antagonism than fecundity or viability selection, and these individual components of fitness tended to reinforce one another to generate even stronger sexual antagonism for net fitness. Traits exhibiting strong sexual dimorphism exhibited greater SA selection than did weakly dimorphic traits, although this pattern was not significant after we controlled for the inclusion of multiple traits nested within species. Our results suggest that intralocus sexual conflict often may persist despite the evolution of sexual dimorphism.

Keywords: intralocus sexual conflict, sexually antagonistic selection, sexual dimorphism, selection differential, selection gradient.

Introduction

Males and females share an autosomal genome and express many of the same phenotypic traits, yet the sexes often have markedly different fitness optima for these shared traits. This sexually antagonistic (SA) selection generates intralocus sexual conflict, because genes that are beneficial when expressed in males are often detrimental when expressed in females. When manifested across multiple loci, this genomic tug-of-war can result in a gender load that neutralizes sexual selection and maintains genetic variation for fitness (Fedorka and Mousseau 2004; Pischedda and

Chippindale 2006; Foerster et al. 2007). Despite its central role in the evolution of sexual dimorphism and its potential generality across sexual mating systems (Badyaev 2002; Bedhomme and Chippindale 2007), intralocus conflict has received much less attention than interlocus conflict (Chapman et al. 2003; Arnqvist and Rowe 2005; Tregenza et al. 2006). In part, this may reflect a general perception that the prevalence of sex linkage, sex-limited gene expression, and sexual dimorphism indicates that intralocus sexual conflict is transient and easily resolved. However, recent studies suggest that sexual dimorphism often fails to resolve intralocus sexual conflict and that fitness costs arising from genomewide conflict can have profound effects on evolutionary dynamics (Pischedda and Chippindale 2006; Bedhomme and Chippindale 2007).

By definition, intralocus sexual conflict can occur only when the selective optimum for a trait differs between the sexes. In sexually dimorphic species, the fact that males and females have achieved sex-specific phenotypic expression suggests that this conflict has perhaps been largely resolved. This raises an intriguing paradox: is sexual dimorphism an indication of prevailing intralocus sexual conflict, or is it the very signature that past conflict has been resolved?

One resolution to this paradox may lie in the relationship between the observed phenotypic distributions and the corresponding selective optima for sexually dimorphic traits (Rice and Chippindale 2001; Bedhomme and Chippindale 2007; Fairbairn 2007). Intralocus sexual conflict will be absent whenever the sexes have identical fitness optima for a monomorphic trait (fig. 1A) or when the observed distributions of a dimorphic trait correspond to the phenotypic optima in each sex (fig. 1D). The former scenario describes sexual monomorphism due to the absence of SA selection, while the latter refers to adaptive sexual dimorphism that resolves latent intralocus sexual conflict. Intralocus conflict persists if males and females remain monomorphic despite SA selection (fig. 1B) or if the degree of sexual dimorphism is less than the sexual

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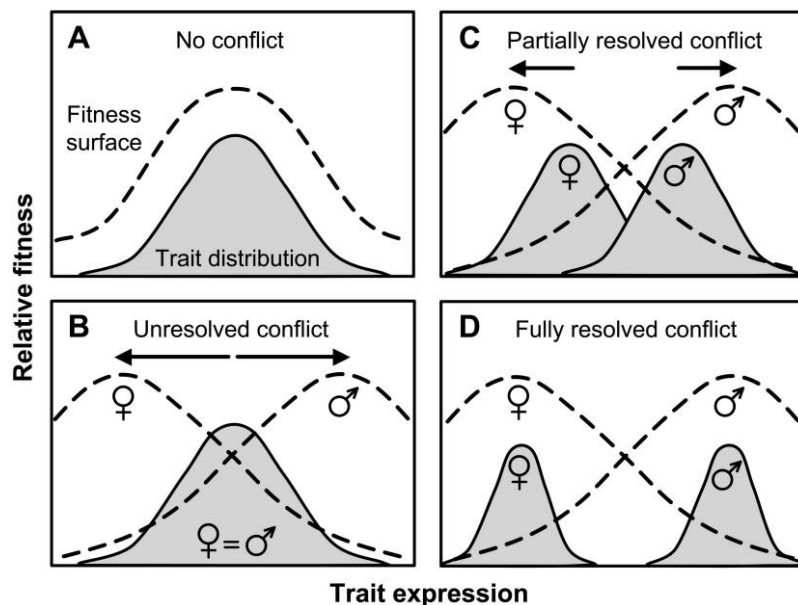


Figure 1: Potential relationships between sexual dimorphism and intralocus sexual conflict. Shaded areas indicate phenotypic distributions for a hypothetical quantitative trait, and dashed lines signify fitness functions for that trait. Arrows indicate the discrepancy between the fitness optimum and the phenotypic mean in each sex. The magnitude of this discrepancy corresponds to the strength of directional selection, and the magnitude of sexually antagonistic directional selection defines the magnitude of unresolved sexual conflict. Adapted from figures in Rice and Chippindale (2001), Day and Bonduriansky (2004), and Bedhomme and Chippindale (2007).

difference in optimal trait expression (fig. 1C). Therefore, the strength of SA selection reflects the inherent potential for intralocus sexual conflict, while the observed degree of sexual dimorphism describes the extent to which this conflict has been successfully resolved by sex-limited trait expression. These issues bear on the fundamental yet unanswered question of whether intersexual genetic correlations present a minor obstacle or a major constraint for the evolution of sexual dimorphism (Lande 1980; Fairbairn and Roff 2006; Bedhomme and Chippindale 2007; Fairbairn 2007). In this study, we use a data set generated by an extensive literature review to address four outstanding questions about SA selection and intralocus sexual conflict.

Is SA Selection Prevalent in Wild Populations?

Although a handful of studies have measured sex-specific fitness surfaces and interpreted their results in the context of sexual-conflict theory (Badyaev and Martin 2000; Badyaev et al. 2000; Preziosi and Fairbairn 2000; Fairbairn 2007), the extent to which intralocus sexual conflict persists in natural populations is generally unknown. Previous literature reviews have generated insight into the strength and form of selection in wild populations (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001; Hereford et

al. 2004), but no comparable analyses exist for SA selection per se.

Is SA Selection Stronger for Reproductive Selection than for Viability Selection?

It is widely thought that sexual dimorphism evolves primarily in response to sexual selection and/or natural selection arising from sex differences in reproductive roles (Darwin 1871; Andersson 1994). For example, sexual selection acting on males and fecundity selection acting on females are two of the primary evolutionary forces thought to underlie the evolution of sexual dimorphism in body size (Cox et al. 2003; Fairbairn et al. 2007). Moreover, quantitative reviews of published selection analyses indicate that the strength of sexual and/or fecundity selection typically exceeds that of viability selection in wild populations (Hoekstra et al. 2001; Kingsolver et al. 2001; Blanckenhorn 2007). This suggests that SA selection arising from differential mating success and/or fecundity may generally be stronger than SA selection arising from differential viability. However, given that the evolution of sexual dimorphism may also reflect niche divergence resulting from selection for different ecological roles in males and females (e.g., Butler et al. 2000, 2007) and that differences in the reproductive roles of males and females

may naturally predispose them to different mortality risks, it is conceivable that viability selection also generates strong sexual antagonism.

Does the Strength of SA Selection Increase as Ontogeny Progresses?

Males and females typically diverge in reproductive roles as ontogeny progresses. Thus, although sexual conflict may occur during juvenile stages (Prasad et al. 2007), the overall strength of SA selection should generally increase through ontogeny (Rice and Chippindale 2001; Badyaev 2002; Sinnero and Calsbeek 2003). In fruit flies (*Drosophila melanogaster*), genomic haplotypes that yield high fitness in juvenile males also yield high fitness in juvenile females. However, SA selection on adult phenotypes reverses this pattern, such that genomes yielding high fitness in adult females impose low fitness on adult males and vice versa (Chippindale et al. 2001; Rice and Chippindale 2001).

Is Sexual Dimorphism Maintained by Current SA Selection?

The magnitude of intralocus sexual conflict depends in part on the extent to which sexual dimorphism is subject to ongoing SA selection (fig. 1). However, it is difficult to make general predictions about the expected relationships between the degree of sexual dimorphism and the strength of SA selection across traits and taxa. If sexual dimorphism generally resolves sexual conflict, then we might predict that large dimorphisms exhibit little current SA selection. Instead, we would expect dimorphic traits to be maintained at their respective optima by sex-specific stabilizing selection (Fairbairn 2007). If sexual conflict persists despite the evolution of sexual dimorphism, then dimorphic traits should be subject to current SA selection (Badyaev and Martin 2000; Badyaev et al. 2000).

Methods

Data Collection

We reviewed published selection gradient analyses from wild animal populations and compiled a database on the strength and form of SA selection acting on a variety of morphological traits. Although SA selection and sexual dimorphism occur in plants (Bond and Maze 1999; Ashman 2003, 2005; Delph et al. 2004, 2005; Maad and Alexandersson 2004; McDaniel 2005; Delph 2007), we restricted our review to studies of animals for ease of comparison. We based this decision in part on the fact that sexual conflict in plants often reflects SA selection on male and female structures that are shared by the same

hermaphroditic individual (Ashman 2003, 2005; Maad and Alexandersson 2004), which differs from the pattern of separate sexes that characterizes our data set for animals. We relied on the extensive compilation of Kingsolver et al. (2001 and <http://hdl.handle.net/10255/dryad.167>) for data published before 1997. We then searched subsequent issues of *American Naturalist*, *Evolution*, and the *Journal of Evolutionary Biology* for selection analyses conducted in wild populations. We supplemented these targeted reviews with an online search of a broader set of journals, using appropriate keywords (sexual conflict, sexually antagonistic selection, selection differential, and selection gradient). Our review was not intended to be exhaustive but rather to generate a large data set containing a variety of traits and taxa.

In our data set, we included only those studies that simultaneously measured selection on shared traits in both sexes in the wild. For each study, we recorded (1) study organism, (2) episode of selection (juvenile viability, adult viability, fecundity, mating success, net selection integrating multiple selective episodes), (3) traits under selection, (4) mean value of the traits in each sex before selection, and (5) standardized linear selection differentials and gradients in each sex. Whenever possible, we recorded sample sizes and standard errors for selection estimates in each sex. When multiple selective episodes were measured in the same study, we calculated net selection across these episodes by assuming that individual selection differentials and gradients were additive (Arnold and Wade 1984). Although this additive partitioning is subject to assumptions about the constancy of phenotypic variance across selective episodes (Wade and Kalisz 1989), it nonetheless provides a useful approximation of overall SA selection arising from multiple fitness components (Badyaev and Martin 2000; Badyaev et al. 2000; Ward 1988).

We also used mean trait values in each sex to calculate an index of sexual dimorphism (SD):

$$SD = \frac{\text{mean trait value in the larger sex}}{\text{mean trait value in the smaller sex}} - 1.$$

This index is based on that of Lovich and Gibbons (1992), the preferred measure of SD in size and other morphological traits (Smith 1999; Cox et al. 2003; Fairbairn et al. 2007). Data are available in appendixes A and B in the online edition of the *American Naturalist*.

Measuring SA Selection

Linear selection differentials and gradients measure the strength of directional selection acting on the mean phenotype, standardized to a mean of 0 in units of standard deviations and estimated separately within each sex. Se-

lection differentials are regression coefficients derived from univariate regressions of fitness against a single trait. As such, they cannot distinguish between direct selection acting on the trait of interest and indirect selection acting through correlated traits (Lande and Arnold 1983; Fairbairn and Reeve 2001). Selection gradients are partial-regression coefficients estimated from multivariate regressions; they quantify the intensity of selection acting on a trait while holding constant the variation due to phenotypic correlations with other traits included in the analysis. Negative values of either gradients or differentials indicate selection favoring a decrease in mean trait value, whereas positive values indicate selection for an increase in mean trait value. Since trait values are independently standardized to units of standard deviation within each sex, there is no inherent tendency for selection differentials and gradients to differ between sexes, assuming equal variance between sexes. Given that our analyses focus on traits that are often highly dimorphic between sexes, standardizing to unit variance is more appropriate than standardizing to trait means within each sex, as has been recommended for other purposes (Hereford et al. 2004).

Previous studies have shown that the strength and direction of differentials and gradients are typically highly congruent across traits and taxa (Hoekstra et al. 2001; Kingsolver et al. 2001). For each question about SA selection, we initially performed separate analyses, using either univariate selection differentials or multivariate selection gradients. We always obtained qualitatively identical results with both approaches, so we report only the results of pooled analyses that include both differentials and gradients. When both were available for a given trait, we included only the multivariate selection gradients in our pooled analyses. Combining differentials and gradients yielded a larger sample of estimates across a greater diversity of traits and taxa.

The definition and measurement of SA selection are subject to debate, so we used several different methods to estimate SA selection, with the explicit goal of describing the potential for intralocus sexual conflict. To quantify overall sexual asymmetries in selection, we calculated the difference between male and female selection differentials or gradients. Thus, if directional selection were significantly positive (e.g., +0.2) for males and negative (-0.2) for females, the resultant difference (0.4) would presumably indicate strong SA selection and high potential for intralocus conflict. However, consider a situation where directional selection on males is strong (+0.4), yet directional selection on females is absent (0). An identical estimate of SA selection (0.4) would be more difficult to interpret with respect to intralocus sexual conflict, since the absence of selection on females would presumably allow the genomes of both sexes to evolve in parallel in

response to selection acting solely on males (Lande 1980). Of course, this would not be the case if females were subject to strong stabilizing (i.e., negative quadratic) selection in addition to the absence of directional selection. Moreover, the absence of selection on females could still generate intralocus sexual conflict by sheltering alleles that subsequently incur a fitness cost when expressed in sons (Day and Bonduriansky 2004). Finally, we could imagine a situation in which selection occurs in the same direction and is strong in both males (+0.6) and females (+0.2), again resulting in an estimate of 0.4 for SA selection. However, this estimate may be misleading in its implication of intralocus sexual conflict, given that selection is acting similarly in each sex. For this reason, we repeated all of our analyses using a modified data set in which we assigned a value of 0 to all estimates for which the direction of selection was the same in each sex, such that any resultant patterns would be driven by purely antagonistic directional selection. In addition to our quantitative measures (above), we qualitatively assessed the presence or absence of SA selection using several criteria: situations in which males and females differed in (1) the sign (direction) of selection differentials or gradients, (2) the direction of selection when the magnitude of selection was at least 0.1 in each sex (an arbitrary benchmark of strong selection), and (3) the direction of selection when differentials or gradients were statistically significant.

Statistical Analyses

Many of the studies that we reviewed contributed several estimates of selection involving multiple traits, replicates, and selection episodes, such that individual data points were clearly not independent in our analyses. When multiple temporal or spatial replicates were reported for a given trait or species (e.g., selection measured in multiple years or across several populations), we calculated the overall mean intensity of selection in each sex by weighting each selection differential by sample size and averaging across replicates. To correct for nonindependence arising from multiple estimates of selection in the same study (e.g., multiple traits within species), we used linear mixed models with species and trait (nested within species) as random effects and predictor variables (e.g., selective episode, ontogenetic stage, and dimorphism category) as fixed effects. Distributions of quantitative SA selection estimates were right-skewed, so we \log_{10} -transformed them before linear mixed model analysis. We supplemented these analyses with nonparametric tests for differences in median SA selection intensity among the same categorical predictor variables. Finally, we used likelihood ratio tests to compare the frequency of SA selection (classified categorically as present or absent on the basis of the first two criteria

discussed above) across these categories. Note that neither our nonparametric tests nor our categorical analyses account for statistical nonindependence due to multiple traits or selective episodes within species.

Large sample sizes are often required for reliable measurement of selection in the wild, and previous reviews have suggested that publication bias and measurement error may result in bias toward larger estimates of selection at low sample sizes (Kingsolver et al. 2001). We did not find any overall trend for the magnitude of SA selection to decrease with sample size ($r^2 < 0.01$, $P = .14$, $n = 416$; data \log_{10} transformed). Likewise, the strength of SA selection was unrelated to sample size for sexual selection ($r^2 < 0.01$, $P = .98$, $n = 90$) and fecundity selection ($r^2 = 0.03$, $P = .084$, $n = 103$). However, SA selection decreased as a function of sample size when only estimates of viability selection were considered ($r^2 = 0.10$, $P < .001$, $n = 156$). To address this potential bias, we supplemented our linear mixed model analyses (above) with identical models in which we weighted observations by sample size. Although it would be preferable to weight estimates by the inverse of their standard error, we chose to weight them by sample size because standard errors were reported for only 29% (123 of 424) of all selection estimates. Weighting observations by sample size never changed the qualitative nature of our results, so we report the results from unweighted analyses unless otherwise noted.

Results

Is SA Selection Prevalent in Wild Populations?

We compiled a data set of 424 selection estimates representing 89 traits in 34 species (table 1; app. A). Across this entire data set, the median of SA selection, calculated as the difference between male and female selection estimates,

was 0.13 (fig. 2A). After controlling for spatial and temporal replication within studies ($n = 203$ estimates; app. B), we obtained a slightly larger median estimate of 0.17 (fig. 2B). Moreover, 25% of the observations exceeded 0.33 in magnitude for both the full and the reduced data sets. Considering only those estimates in which the direction of selection was opposite in males and females, we found substantially larger median values of 0.30 for SA selection across all studies ($n = 175$; fig. 2A) and of 0.31 after correcting for spatial and temporal replication ($n = 80$; fig. 2B).

If we define SA selection as a difference in the direction of selection on males and females, then 41% (175 of 424) of the estimates exhibited SA selection when all temporal and spatial replicates were considered. When replication within studies was controlled for, 39% (80 of 203) of the estimates exhibited SA selection. Considering only those studies in which the magnitudes of opposing selection differentials and gradients were at least 0.1 in each sex, we obtained a more conservative estimate of the frequency of SA selection, 17% in both our full data set (73 of 424) and after controlling for replication (34 of 203). Finally, 10% (43 of 424) of the observations in our full data set consisted of statistically significant selection in one sex and opposing selection (even if nonsignificant) in the opposite sex. However, only 3% (13 of 424) of all observations provided evidence of statistically significant selection in opposite directions in each sex, and seven of these estimates were derived from a single species (*Carpodacus mexicanus*; Badyaev and Martin 2000; Badyaev et al. 2000).

Is SA Selection Stronger for Reproductive Selection than for Viability Selection?

Across 164 observations representing 79 traits from 30 species, median SA selection was weakest for viability selection, intermediate for fecundity selection, and strongest

Table 1: Summary of literature review data set, partitioned by taxon and selective episode

Selective episode	Vertebrates			Invertebrates			All taxa		
	Estimates	Traits	Species	Estimates	Traits	Species	Estimates	Traits	Species
Viability selection	117	46	14	39	12	4	156	58	18
Fecundity selection	101	36	9	4	3	2	105	40	11
Sexual selection	77	17	7	18	10	8	95	27	15
Fecundity/sexual selection	8	8	3	20	10	3	28	18	6
Net selection	14 (34)	7 (34)	4 (12)	26 (13)	7 (13)	1 (5)	40 (47)	14 (47)	5 (17)
All selective episodes	317	68	22	107	21	12	424	89	34

Note: "Estimates" refers to the total number of available observations and includes temporal and spatial replicates of selection on individual traits (i.e., the "full data set"). "Traits" refers to the total number of traits measured across all species and also corresponds to the number of observations after temporal and spatial replicates are removed. "Fecundity/sexual selection" refers to data for which sexual antagonism was assessed on the basis of fecundity of females and mating success of males. For net selection, numbers not in parentheses report estimates from original publications and include multiple spatial and temporal replicates; numbers in parentheses include our additive estimates of net selection and report only one estimate per trait to correct for temporal and spatial replication.

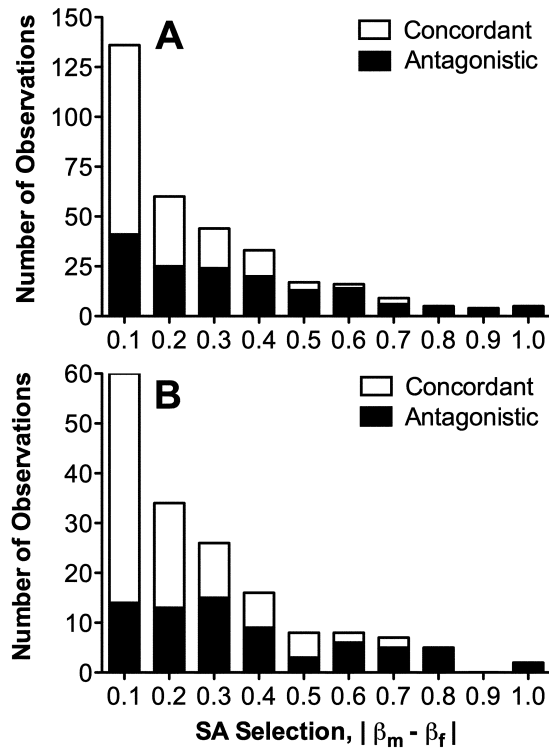


Figure 2: Frequency distributions for sexual differences in directional selection differentials and gradients across all spatial and temporal replicates (A) and after removing spatial and temporal replicates within species (B). Data are separated into measurements in which males and females differed in the direction of selection (antagonistic, filled bars) or in which selection acted in the same direction in both sexes (concordant, open bars). Data are binned at intervals of 0.1 standard deviations (bins contain all values below axis value), and plots are truncated at 1.0 for visual clarity. SA = sexually antagonistic.

for sexual and net selection (Kruskal-Wallis: $\chi^2 = 22.83$, $P < .0001$; fig. 3A). Mean SA selection followed a similar pattern even after species and trait (nested within species) were included as random factors (linear mixed model: $F = 15.80$, $df = 3, 116$, $P < .0001$; fig. 3B). This result remained highly significant even after selection estimates were weighted by sample size (linear mixed model: $F = 18.19$, $df = 3, 114$, $P < .0001$). To verify that these patterns were not simply driven by sexual differences in the relative strength of selection acting in the same direction, we repeated these analyses after assigning a value of 0 to all estimates in which the direction of selection was the same in each sex. These analyses verified that sexual selection and net selection exhibited the greatest sexual antagonism (Kruskal-Wallis: $\chi^2 = 13.12$, $P = .004$; linear mixed model weighted by sample size: $F = 9.37$, $df = 3, 114$, $P < .0001$). Moreover, the proportion of observations in which selection acted in opposite directions on males and

females was significantly higher for estimates of sexual and net selection than for fecundity or viability selection (likelihood ratio: $\chi^2 = 11.38$; $P = .001$; fig. 3C). This result approached statistical significance even when we used a more stringent categorization of sexual antagonism as selection acting in opposite directions and with a magnitude of at least 0.1 in each sex ($\chi^2 = 6.95$, $P = .073$).

When we pooled estimates of fecundity and sexual se-

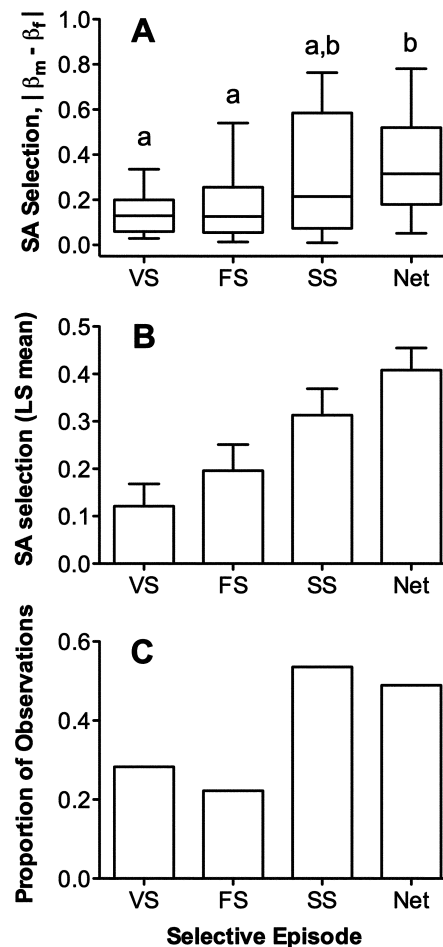


Figure 3: Sexually antagonistic (SA) selection as a function of selective episode: VS = viability selection; FS = fecundity selection; SS = sexual selection; Net = total selection integrating multiple selective episodes. A, Box-and-whisker plots (median, twenty-fifth to seventy-fifth percentile, and tenth to ninetieth percentile) expressing SA selection as the difference between selection gradients in males and females. Lowercase letters indicate statistical separation based on Kruskal-Wallis tests with Dunn's multiple-comparison post hoc tests. B, Least squares means (+1 SE) of SA selection estimated from linear mixed models including species and trait (nested within species) as random effects. Data were \log_{10} transformed before analysis, but actual values are shown for illustrative purposes. C, Frequency of SA selection expressed as the proportion of observations in which selection acted in opposite directions in males and females.

lection into a single category reflecting differential reproduction, we found that net selection generated greater SA than reproductive selection or viability selection alone (Kruskal-Wallis: $\chi^2 = 17.76$, $P < .0001$). This result was consistent regardless of whether we analyzed all available data ($n = 197$ observations, 85 traits, 34 species; linear mixed model: $F = 19.60$, $df = 2, 137$, $P < .0001$; weighted by sample size: $F = 22.03$, $df = 2, 117$, $P < .0001$) or conducted more conservative analyses in which we (1) included only the subset of studies for which both reproductive and viability selection were measured on the same traits ($n = 147$ observations, 41 traits, 14 species; linear mixed model: $F = 18.85$, $df = 2, 117$, $P < .0001$) or (2) included only those studies for which net selection was estimated directly by the authors in nonadditive fashion ($n = 51$ observations, 12 traits, 3 species; linear mixed model: $F = 4.35$, $df = 2, 37$, $P = .02$). After assigning a value of 0 to all observations in which the direction of selection was the same in each sex, we still observed the greatest SA arising from net selection and the lowest SA arising from viability selection (Kruskal-Wallis: $\chi^2 = 6.33$, $P = .042$; linear mixed model weighted by sample size: $F = 12.95$, $df = 2, 117$, $P < .0001$).

Does the Strength of SA Selection Increase as Ontogeny Progresses?

We compared the strength of SA selection as a function of ontogeny across 149 observations representing 78 traits from 31 species. We did not find an overall difference in the median strength of SA selection when comparing selection for juvenile viability with selection for adult viability (Wilcoxon: $\chi^2 = 2.12$, $P = .15$) or selection for adult reproduction (Wilcoxon: $\chi^2 = 0.06$, $P = .82$). We obtained similar results when comparing mean SA selection between ontogenetic stages after accounting for species and traits (nested within species) as random factors (linear mixed models: $P > .3$ for all comparisons). After categorizing SA selection binomially (present if the direction of selection differed between sexes, absent otherwise), we actually found a slightly greater frequency of SA selection resulting from juvenile viability relative to adult viability (likelihood ratio: $\chi^2 = 3.91$, $P = .048$). This weak effect was also observed when we used this criterion to assign a value of 0 to instances in which SA selection was absent and when we retained quantitative measures when SA selection was present (Wilcoxon: $\chi^2 = 4.09$, $P = .043$; linear mixed model weighted by sample size: $F = 3.50$, $df = 1, 38$, $P = .069$). In part, this unexpected result may reflect the fact that we obtained very few estimates of juvenile viability selection (14 traits in four species) after controlling for spatial and temporal replication within studies. These patterns were not evident

when we used a more stringent criterion that considered SA selection to be present only when the magnitude of selection was at least 0.1 in each sex ($P < .4$ for all analyses). Moreover, we did not detect any difference in the frequency or magnitude of SA selection when comparing juvenile viability and adult reproduction with any of the above methods ($P < .3$ for all analyses).

After including all replicates within studies, we found no support for an ontogenetic component to SA selection using estimates of juvenile and adult viability that were measured for the same trait in the same species (Wilcoxon matched-pairs test: $P = .43$, $n = 24$ comparisons). However, when we conducted a paired comparison of juvenile viability selection and adult reproductive selection, we found slightly stronger SA selection during adult reproduction (Wilcoxon matched-pairs test: $P = .044$, $n = 19$ comparisons). This result provides weak support for a tendency toward an increase in SA selection as ontogeny progresses, although it is derived from only 11 independent traits in two species.

Is Sexual Dimorphism Maintained by Current SA Selection?

Overall, the degree of SA selection was positively correlated with the magnitude of sexual dimorphism (SD), although most of the variance in SA selection was unrelated to SD ($r^2 = 0.04$, $P = .002$, $n = 232$ observations; data \log_{10} transformed). However, we found no evidence of a relationship between SA selection and SD after correcting for temporal and spatial replication and including species and trait (nested within species) as random factors (linear mixed model: $F = 1.91$, $df = 1, 60$, $P = .17$, $n = 138$ observations, 55 traits, 22 species). We obtained the same result even when considering only estimates of net selection (linear mixed model: $F = 0.67$, $df = 1, 22$, $P = .42$, $n = 25$ traits, 12 species), which shows the strongest sexual antagonism (above) and presumably provides the best measure of total selection for SD.

We also compared the median intensity of SA selection across three arbitrary categories corresponding to slight ($SD < 0.03$), moderate ($0.03 \leq SD \leq 0.10$), or strong ($SD > 0.10$) SD. We classified the direction of SA selection as positive if it favored the observed dimorphism and negative if it opposed the dimorphism and then used Wilcoxon signed-rank tests to determine whether median SA selection differed from 0 within each category (fig. 4A). The median magnitude of SA selection did not differ from 0 for traits exhibiting slight dimorphism ($W = 16$, $n = 36$, $P = .81$) but acted in the direction of observed sexual differences for both moderate ($W = 340$, $n = 68$, $P = .037$) and strong dimorphisms ($W = 130.5$, $n = 34$, $P = .017$). However, these latter two comparisons are only

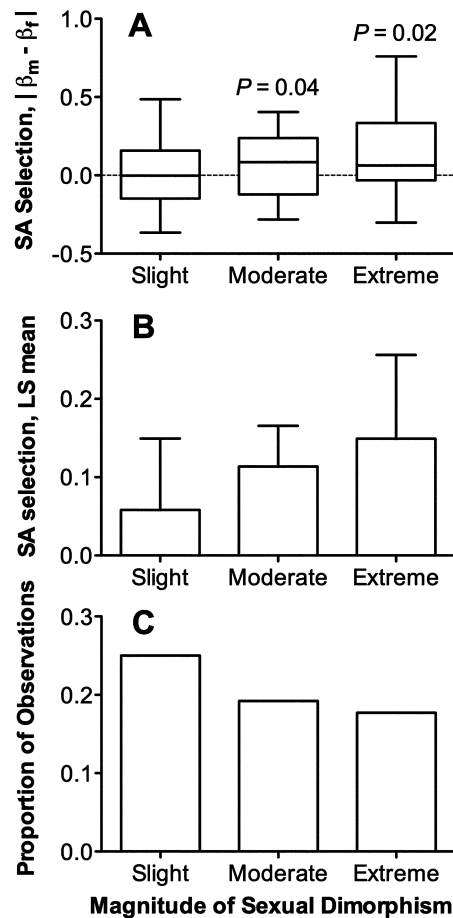


Figure 4: Sexually antagonistic (SA) selection as a function of sexual dimorphism (SD), categorized as slight ($SD < 0.03$), moderate ($0.03 \leq SD \leq 0.1$), and strong ($SD > 0.1$). *A*, Box-and-whisker plots (median, twenty-fifth to seventy-fifth percentile, and tenth to ninetieth percentile) expressing SA selection as the difference between selection gradients in males and females. Estimates were assigned positive values when SA selection favored an increase in observed sexual dimorphism. Statistics are reported for Wilcoxon signed-rank tests to determine whether median SA selection differed from 0 within each category. *B*, Least squares means ($+1$ SE) of SA selection estimated from linear mixed models including species and trait (nested within species) as random effects. Data were \log_{10} transformed before analysis, but actual values are shown for illustrative purposes. *C*, Frequency of SA selection expressed as the proportion of observations in which selection acted in opposite directions in males and females and favored the observed dimorphism.

marginally significant after adjustment of the overall significance level for three independent comparisons (Bonferroni correction: $\alpha = 0.017$). Moreover, we found no evidence of a difference in the strength of SA selection across these categories after including species and trait (nested within species) as random factors (linear mixed model: $F = 0.23$, $df = 1, 10$, $P = .80$, $n = 138$ observations, 55 traits, 22 species; fig. 4*B*). The proportion of

observations in which selection acted in opposite directions on males and females did not differ across these SD categories (likelihood ratio: $\chi^2 = 2.26$, $P = .32$; fig. 4*C*), nor did it differ when SA selection was recognized only when the magnitude of opposing selection was at least 0.1 in each sex (likelihood ratio: $\chi^2 = 0.81$, $P = .67$). Finally, we found no difference in SA selection across these SD categories when assigning a value of 0 when the direction of selection was the same in each sex ($P > .6$ for Kruskal-Wallis and linear mixed model analyses).

For studies involving at least three independent morphological traits, we ranked the direction and intensity of SA selection and the direction and magnitude of SD for each trait and then estimated the slope of the relationship between these ranks within each species (see Badyaev et al. 2000). When multiple selective episodes or spatial/temporal replicates were available for a given species, we used estimates of net selection or the mean intensity of SA selection across episodes and replicates to avoid bias due to multiple measures from the same system. Each of the eight studies that we analyzed revealed a positive correlation between the degree of trait dimorphism and the intensity of SA selection. While these rank-order correlations were generally not significant within each species because of the small number of traits under consideration (range 3–8), the overall mean slope across studies was significantly greater than 0 (mean ± 1 SD = 0.62 ± 0.28 , $t = 6.28$, $P < .001$).

Discussion

Is SA Selection Prevalent in Wild Populations?

The median difference in selection between males and females was 0.17 across all traits and studies after we controlled for spatial and temporal replication. This is analogous to selection driving the sexes apart by 0.17 standard deviations per selective episode. However, we emphasize that our measure of SA selection does not describe within-generation change in trait means in the same manner as a selection differential. One additional caveat to this analysis is that our use of absolute values to derive the frequency distribution of SA selection is subject to bias that will systematically overestimate the strength of selection (Hereford et al. 2004). Even if selection were entirely absent, measurement error would produce a scatter of positive and negative estimates converging on 0, and the transformation of this random error to absolute values would give the erroneous impression that selection intensity was greater than 0 (Hereford et al. 2004).

As a supplemental approach, we categorized SA selection as a difference in the direction of selection in each sex and considered only those instances in which the

strength of such antagonism was at least 0.1 in each sex. Using this approach, we found that 17% of available estimates exhibited sexual antagonism (fig. 2). When we considered only these estimates, the median strength of SA selection was 0.3 across all traits. Thus, it appears that SA selection is common (though clearly not ubiquitous) and often quite strong in wild populations. However, we note that only 3% of available estimates reported statistically significant selection that differed in direction between the sexes. This apparent lack of support for SA selection may, in part, reflect the fact that most studies did not explicitly test for sexual differences in selection (i.e., sex-by-trait interactions that influenced fitness). In many cases, such interactions could be present even when selection estimates are not significant within either sex. We suggest that future studies should explicitly test for sexual differences in the form and intensity of selection. Moreover, it is difficult to assess the actual prevalence of SA selection even within the selection literature, given that many studies of highly dimorphic traits focus only on selection in one sex (e.g., 14 of 50 studies in the data set of Kingsolver et al. [2001] focus on a single sex), whereas many studies of monomorphic traits combine males and females for analysis (e.g., 16 of 50 studies in this same data set pool sexes for analysis).

Is SA Selection Stronger for Reproductive Selection than for Viability Selection?

Selection arising from variance in reproduction (i.e., sexual and fecundity selection) exhibited a greater magnitude of sexual antagonism than selection arising from differential viability. This trend was driven primarily by estimates of sexual selection, which generated stronger sexual antagonism than either viability or fecundity selection (fig. 3). This result was consistent across all available data (fig. 3A), after effects due to species and multiple traits nested within species were removed (fig. 3B), and when SA selection was dichotomized on the basis of the direction of selection in each sex (fig. 3C). These results agree with previous analyses suggesting that selection is generally stronger when arising from differential mating success and fecundity than when arising from differential viability (Hoekstra et al. 2001; Kingsolver et al. 2001; Blanckenhorn 2007).

Estimates of net selection incorporating multiple selective episodes generally revealed stronger sexual antagonism than estimates that decomposed selection into individual episodes (i.e., viability, fecundity, and mating success). Although the magnitude of net SA selection was only slightly greater than that arising from sexual selection alone, it is interesting that the additional contributions of fecundity and viability selection tended to exacerbate sexual antagonism rather than to counteract the effects of sexual se-

lection. This underscores the importance of integrating multiple selective episodes to estimate net lifetime fitness when assessing SA selection in wild populations (Fairbairn 2007).

Does the Strength of SA Selection Increase as Ontogeny Progresses?

We did not find an overall difference in the strength of SA selection when comparing selection for juvenile viability with selection for adult viability or adult reproduction. However, when we conducted a paired analysis comparing juvenile viability selection with adult reproductive selection within a subset of species for which both estimates were available, we found significantly stronger SA directional selection during adult reproduction. This provides some support for a tendency toward increasing SA selection as ontogeny progresses, a result predicted by theory and observed empirically in some species (Chippindale et al. 2001; Rice and Chippindale 2001). However, this result is derived from only 11 independent traits in two species. In general, estimates of sex-specific juvenile selection were relatively uncommon. This may reflect a tendency for researchers to combine data from juvenile males and females for analysis, either because sex identification is problematic before adulthood (Merilä et al. 1998) or because SA selection is either assumed or verified to be absent. Any such bias could prevent nonsignificant SA selection from being reported for juveniles.

Is Sexual Dimorphism Maintained by Current SA Selection?

Overall, the degree of SA selection was positively correlated with the magnitude of sexual dimorphism in morphological traits. Monomorphic or weakly dimorphic traits exhibited no consistent pattern of SA selection, whereas moderate and highly dimorphic traits were subject to current SA selection that favored increased sexual dimorphism (fig. 4A). This suggests that sexual dimorphism is often subject to ongoing SA selection, possibly indicating a general potential for unresolved intralocus sexual conflict across diverse traits and taxa. However, this result was not observed after we controlled for multiple replicates and traits within studies (fig. 4B). Thus, our results are ambiguous with respect to the relationship between sexual dimorphism and current selection. Recent studies are also equivocal on this issue. Positive correlations between population fitness and sexual dimorphism are consistent with the interpretation that the evolution of sexual dimorphism liberates seed beetles (*Callosobruchus maculatus*) from the gender load imposed by SA selection (Rankin and Arnqvist 2008). However, a suite of experiments on fruit flies (*Dro-*

sophila melanogaster) suggest that intralocus sexual conflict persists despite the evolution of sexual dimorphism (Pischedda and Chippindale 2006; Bedhomme and Chippindale 2007).

Case Studies of SA Selection and Intralocus Sexual Conflict

Our analyses suggest that SA selection and resultant intralocus sexual conflict may be common in wild populations, but it is difficult to evaluate the prevalence of the respective scenarios in figure 1 on the basis of these data alone. Interestingly, case studies of SA selection provide empirical examples of each of these hypothetical scenarios. As might be intuitively predicted, sexual monomorphism often corresponds to the absence of SA selection (fig. 1A). For example, sexually monomorphic traits experience similar net selective pressures in male and female house finches (*Carpodacus mexicanus*), whereas sexually dimorphic traits are subject to SA selection (Badyaev and Martin 2000; Badyaev et al. 2000).

Sexual monomorphism may also persist despite strong SA selection favoring dimorphism (fig. 1B). Collared flycatcher (*Ficedula albicollis*) males and females are similar in size despite SA selection favoring small size in male nestlings and large size in female nestlings (Merilä et al. 1997). This suggests that differential juvenile viability leads to adult sexual dimorphism that is purely phenotypic, in the sense that it is perpetually eroded by the strong intersexual heritability of size such that each new generation reverts to monomorphism (Merilä et al. 1997, 1998). However, the absence of sexual dimorphism in this case may actually reflect temporal variation in selection and/or selection on the nonheritable portion of phenotypic variation rather than unresolved conflict per se (Kruuk et al. 2001).

Water striders (*Aquarius remigis*) exhibit moderate sexual dimorphism in body size, and net lifetime fitness functions indicate that stabilizing selection maintains male and female body sizes at their respective phenotypic optima (Preziosi and Fairbairn 2000; Fairbairn 2007). In this example, current sexual dimorphism appears to resolve sexual conflict over body size (fig. 1D). Yellow-pine chipmunks (*Tamias amoenus*) also exhibit moderate sexual size dimorphism, but in this case, only males appear to be at their ecological optimum for body size. Females remain under directional selection for increased size (Schulte-Hostedde et al. 2002), suggesting that unresolved sexual conflict is impeding the evolution of adaptive sexual size dimorphism by holding females below their ecological fitness optimum.

In other dimorphic species, directional selection is strong in both sexes and acts in opposite directions, in-

dicating that sexual conflict persists despite the evolution of sexual dimorphism (fig. 1C). Fitness of male zebra finches (*Taeniopygia guttata*) increases with the intensity of red bill color because of strong female preference for redder bills, whereas females with red bills experience reduced survival relative to those with orange bills (Price and Burley 1994). Similarly, body size and bill morphology are subject to SA selection in the house finch (*C. mexicanus*; Badyaev and Martin 2000; Badyaev et al. 2000). Despite the evolution of sexual dimorphism, both sexes remain far from their ecological optima, presumably because of unresolved sexual conflict arising from strong intersexual genetic correlations (Badyaev and Martin 2000).

Sexual conflict may also occur at loci for discrete polymorphisms. Insular populations of adders (*Vipera berus*) express a dorsal color polymorphism, with individuals exhibiting either melanistic or “zig-zag” patterns (Forsman 1995). Whereas zig-zag males have higher annual survival than melanistic males, the pattern is reversed in females. Other examples of sex-specific selection on color polymorphisms occur in marine isopods (Jormalainen et al. 1995), butterflies (Kingsolver 1996), grasshoppers (Forsman and Appelqvist 1999), and lizards (Forsman and Shine 1995), suggesting that color polymorphism may often be a transient evolutionary stage in the resolution of sexual conflict via sex linkage or hormonal regulation of sexual dichromatism.

Sexual antagonism may also result from correlational selection acting on trait combinations rather than on individual traits per se. Viability selection favors a late date of eclosion to the adult stage in both male and female water striders (*A. remigis*), but whereas males that eclose late in the season attain maximal fitness at small body sizes, females that eclose late attain maximal fitness at large body sizes (Ferguson and Fairbairn 2000). Viability selection favors a negative phenotypic correlation between stamina and immune function in male lizards (*Anolis sagrei*), whereas females experience selection for increased stamina and immune function (Calsbeek and Bonneaud 2008). A similar situation is observed in the serin (*Serinus serinus*), where viability selection favors a negative phenotypic correlation between wing and tail lengths in males and a positive association between these same traits in females (Björklund and Senar 2001). Male and female dark-eyed juncos (*Junco hyemalis*) experience antagonistic selection on wing length, but selection acting on the interaction between wing length and the size of white tail patches favors positive trait correlations in each sex (McGlothlin et al. 2005). In this example, correlational selection may mitigate intralocus conflict by favoring similar genetic correlations in each sex, despite SA selection on individual traits.

Although most selection studies focus on particular traits, perhaps the most valuable information regarding intralocus sexual conflict will come from investigations of the intersexual heritability of overall fitness. Several recent studies have shown that genomewide sexual conflict can result in the production of high-quality offspring of the same sex but low-quality offspring of the opposite sex (Fedorka and Mousseau 2004; Pischedda and Chippindale 2006; Foerster et al. 2007). This phenomenon may be a general feature of sexual mating systems, potentially overwhelming the fitness benefits of sexual selection (Pischedda and Chippindale 2006) and maintaining genetic variation for fitness even in the face of strong selection (Foerster et al. 2007). With genetic paternity analyses now commonplace, it should be possible to test for reversed inheritance of fitness across sexes in many wild populations. We predict that these approaches will reveal that SA selection and resultant intralocus sexual conflict are prevalent across diverse taxa and mating systems, with important implications for a variety of evolutionary processes.

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