

ORIGINAL ARTICLE

The evolutionary genetics of sexual size dimorphism in the cricket *Allonemobius socius*KM Fedorka¹, WE Winterhalter¹ and TA Mousseau²¹Department of Biology, University of Central Florida, Orlando, FL, USA and ²Department of Biological Sciences, University of South Carolina, Columbia, SC, USA

In recent years, investigations into the evolution of sexual size dimorphism have moved from a simple single trait, single sex perspective, to the more robust view of multivariate selection acting on both males and females. However, more accurate predictions regarding selection response may be possible if some knowledge of the underlying sex-specific genetic architecture exists. In the striped ground cricket, *Allonemobius socius*, females are the larger sex. Furthermore, body size appears to be closely associated with fitness in both males and females. Here, we investigate the role that genetic architecture may play in affecting this pattern. Employing a quantitative genetic approach, we estimated the sex-specific selection gradients and the (co)variance matrix for body size and wing morphology (that is, either a long-winged flight-capable phenotype or a short-winged flightless phenotype) to predict

phenotypic change in the next generation. We found that the sexes differed significantly in their selection gradients as well as several of their genetic parameters. Our predictions of next-generation change indicated that the within-sex genetic correlations, as well as the between-sex genetic correlations, should play a significant role in sexually dimorphic evolution in this system. Specifically, the female size response was increased by approximately 178% when the between-sex genetic correlations were considered. Thus, our predictions reinforce the notion that genetic architecture can produce counterintuitive responses to selection, and suggest that even a complete knowledge of the selection pressures acting on a trait may misrepresent the trajectory of trait evolution.

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Introduction

Sexual size dimorphism (SSD) or the difference in mean size between the sexes is widely observed throughout the animal kingdom. Adaptive evolution of SSD is generally explained through three hypotheses (Hedrick and Temeles, 1989). First, dimorphism via sexual selection may occur when individuals of a particular size in one sex are differentially successful via mate choice or mate competition (Andersson, 1994). Slatkin (1984) suggested that dimorphism may also be maintained through purely ecological mechanisms. In this model the sexes occupy different fitness optima for a certain trait, creating dimorphic niches. These different niches may originate through direct competition for resources (where dimorphism itself is adaptive), or through divergent ecological roles. Finally, dimorphism may be maintained through differential reproductive selection. The most common reproductive model, the fecundity advantage model, suggests that large female size is strongly associated with a greater reproductive output (Shine, 1988).

Early investigations into the maintenance of female-biased SSD centered on this latter hypothesis (Cluttonbrock and Harvey, 1978; Berry and Shine, 1980; Gilbert and Williamson, 1983). Unfortunately, these studies generally ignored selection on male body size, which can contribute equally to the dimorphic pattern. Furthermore, other selective pressures may be acting differentially on female body size over time, which can considerably modify the relationship between size and fitness. Thus, research over the past decade has focused on generating a more robust view of selection by examining the interplay between differing selective pressures acting on both sexes to estimate the net selective force (Price, 1984; Ferguson and Fairbairn, 2000; Preziosi and Fairbairn, 2000). However, even a complete knowledge of selection has limits when attempting to predict next-generation phenotypic change.

To this end, some knowledge of the underlying sex-specific genetic architecture for body size is needed. The reasons for this are manifold. First, body size can only respond to selection if sufficient genetic variation exists in the population (Roff, 1997). Second, a dimorphic response in size is possible only if the genetic correlation between the sexes for the homologous trait is less than one, indicating the existence of sex-specific genetic variation (Lande, 1980; Via and Lande, 1985; Ashman, 2005). Third, genetic correlations within each sex may modify the magnitude and/or direction of the body size

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response (Roff, 1997). Fourth, even if ample genetic variance for body size exists and genetic correlations are less than one, the overall genetic architecture may still constrain evolution by limiting the amount of genetic variance that exists in the multivariate direction of selection (Blows and Hoffmann, 2005). Therefore, just as the dynamics between differing selective pressures are important in determining net selective force, the dynamics between selection and the underlying genetic structure may provide valuable insights regarding the evolution of a dimorphic trait (Ashman, 2005).

In the striped ground cricket, *Allonemobius socius*, females are the larger sex. Furthermore, body size appears to be significantly associated with both male mating success and female reproductive success (Fedorka and Mousseau, 2002a, b). As with most sexually dimorphic systems, however, little is known regarding the role that genetic architecture plays in dimorphism. To this end, we employed a quantitative genetic design, coupling sex-specific selection gradients with h^2 -matrices (standardized form of the G-matrix comprised of trait heritabilities and additive genetic correlations) for body size and wing morphology (that is, either a long-wing flight-capable phenotype or a short-wing flightless phenotype). This allowed us to first estimate the amount of additive genetic variance for body size; second, compare the sexes for differences in genetic parameters; third, test for significant correlations between the sexes for homologous traits; and fourth, model the response to selection in order to assess the potential influence that genetic architecture may have on dimorphic evolution.

Methods

Selection gradients (β) and additive genetic variance and covariances (G) form the basis of modeling microevolutionary change in accordance with quantitative genetic theory (Lande and Arnold, 1983; Roff, 1997). Thus, the evolutionary trajectory of body size may be significantly influenced by its genetic associations with other traits under selection. Previous work suggests that wing morphology represents a potentially important correlated character. Evidence from other cricket systems suggests that the long-winged morph is negatively associated with both male mating success (Roff *et al.*, 2003) and female fecundity (Stirling *et al.*, 2001). In contrast, body size in *A. socius* is positively associated with male mating success and female reproductive success (Fedorka and Mousseau, 2002a). However, large body size is associated with the short-winged morph in females (Mousseau, 1988; Roff, 1995), but the long-winged morph in males (Mousseau, 1988). If male and female *A. socius* exhibit different genetic parameters for these characters but similar selection regimes, then counterintuitive selection responses may result.

Experimental design

Estimation of selection gradients: *A. socius* is a small chirping ground cricket that ranges throughout the southeastern United States, with closely related sister taxa extending across North America (Howard and Furth, 1986; Mousseau and Roff, 1989). Adult crickets (approximately 200) were collected in the fall of 1999 near Asheville (NC, USA). Females were placed separately into plastic cages along with an adult male.

Cages were 10 × 10 × 8 cm and contained ground cat food and a carrot slice (provided in excess), dampened cheesecloth (water source and oviposition material) and strips of brown paper towel for cover. Every 2 days, the food, carrot and paper towel were replaced. Cages were kept in a constant environment at 28°C and a 12:12 (L:D) photoperiod provided by a Percival incubator (Boone, IA, USA). Eggs were collected and offspring were reared in the same environment as the parental generation. Upon adult eclosion the sexes were separated and maintained as virgins at low density (4–5 per cage). Age of experimental crickets was 10 ± 2 days post eclosion.

To estimate selection on each sex, we regressed femur length (estimate of body size) and wing morph (long- and short-winged coded as 1 and 0, respectively) against relative fitness. Characters were standardized to a mean of zero and unit variance and relative fitness was calculated as $\omega_{\text{relative}} = \omega_{\text{individual}} / \omega_{\text{average}}$ (Fedorka and Mousseau, 2002a). Fitness estimates were based on mating success for males and reproductive success for females. Both univariate (β'_X) and multivariate (β_X) selection gradients were calculated for each sex-specific trait. Multivariate gradients were estimated via a standardized partial regression, allowing us to disentangle direct from indirect selection (Lande and Arnold, 1983).

To assess male mating success and female reproductive success, two unrelated males were placed into a mating arena (100 mm Petri dish) along with a randomly chosen, unrelated female. Each male ($n = 220$) was tested on average five times against a different male with a new virgin female used for each trial ($n = 1067$). Thus, the male estimate of fitness was based on the proportion of successful mating attempts and female fitness was based on the number of eggs produced. These estimates of fitness do not consider selection associated with dispersal of the long-winged morph. However, dispersal selection is likely to be minor compared with the reproductive selection acting on male mating success and female fecundity. To help control for the potential influence of mating experience, males were tested against other males who shared an equal number of previous trials (that is 0, 1, 2, ...). After mating, the female was isolated to oviposit until her death. Females who produced no eggs were assigned a fecundity of zero. Femur length and wing morphology were recorded after mating and oviposition were complete.

Estimation of genetic architecture: To estimate the sex-specific (co)variance matrix of body size and wing morphology, we employed a quantitative genetic half-sib family (with nested full-sibs) design. The parental generation originated from the same population near (Asheville, NC, USA) and was collected in the fall of 2001. Approximately, 200 adult crickets were brought back to the lab and reared under common garden conditions (27°C; 9L:15D photoperiod) for two generations to remove any potential maternal effects (Mousseau and Dingle, 1991; Mousseau and Fox, 1998). Upon completion of the second generation, a single sire was mated to three randomly selected dams thereby producing a series of full-sib families nested within half-sib families. Resulting eggs were placed into diapause at 5°C to simulate winter conditions and ensure hatching

synchrony. Eggs were removed in two distinct groups (batches) after 4 and 6 months of simulated winter conditions. In view of a two-factor ANOVA, neither body size or wing morphology differed significantly between the batches (body size: $F_{1,1172}=0.87$; $P=0.927$; wing morphology: $F_{1,1253}=0.47$; $P=0.4917$), nor did batch interact significantly with gender (body size: $F_{1,1172}=0.01$; $P=0.9218$; wing morphology: $F_{1,1253}=0.03$; $P=0.8723$). As such, the two batches were pooled before estimating the genetic parameters.

Following the completion of diapause, hatchlings between 5 and 25 from each nested full-sib family were reared under temperature and photoperiod conditions that mirrored the average fluctuations found in Florence (SC, USA; Figure 1). Cages were maintained every other day as above, and at 4 weeks each cage was split to reduce potential crowding effects. Adults were harvested every 5 ± 1 days, whereupon they had their femur length and wing morph recorded. Because wing morphology is a dichotomous trait, the proportion of long-winged individuals was calculated for each nested dam (that is, full-sib family) and angularly transformed before the analyses.

Sex-specific genetic-matrices were estimated using restricted maximum likelihood methodologies (PROC MIXED; SAS 9; 1 January 2003). Standard errors of all matrix elements were based on jackknifed pseudo-values (Begin *et al.*, 2004). Such estimates have been found to accurately represent the variation even when sample sizes are unbalanced (Rolf and Preziosi, 1994). Significance tests were based on these standard errors using a single-value *t*-test (Sokal and Rohlf, 1995). To test for

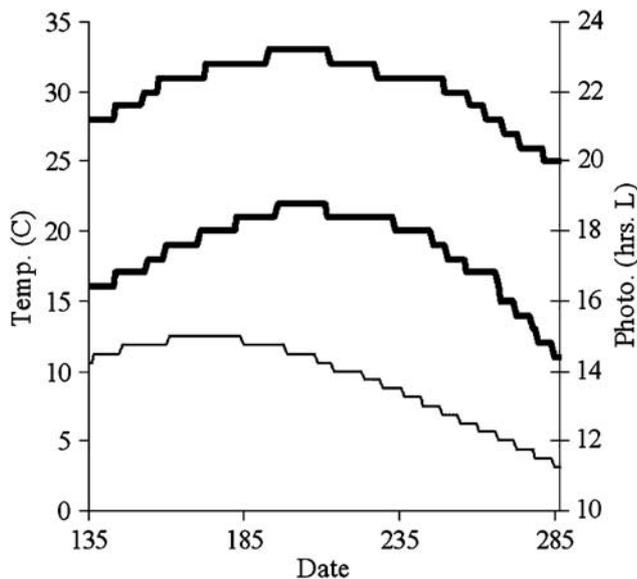


Figure 1 Temperature and photoperiod regimes used for the estimation of genetic parameters. Daily high (upper line) and low (middle line) temperatures are in °C and photoperiods (lower line) are in hours of light. The x axis is scaled to the number of days into the experiment and the Julian date on which the conditions were based (that is the first day of the experiment was based on day 135 in the natural environment). All data were based on the average conditions found in Florence, (SC, USA) and obtained from local weather stations (EarthInfo Inc., 1997, Boulder CO, USA) and the Naval Observatory's sunrise-sunset tables (US Navy, 2005; <http://www.usno.navy.mil/>).

significant differences between male and female architecture, we employed an element-by-element comparison using *t*-tests based on the jackknifed pseudo-values. Owing to variation in reproductive output among dams and survivorship among nymphs, sample sizes were unbalanced. A total of 1176 individuals distributed across 117 full-sib families and nested within 47 half-sib families were available for our estimations.

Response to selection: To model the evolution of SSD, we coupled the heritability matrix (standardized form of the G-matrix comprised of trait heritabilities and genetic correlations) with the selection gradients to predict next generation change in body size, R_B , for each sex such that

$$R_B[\varnothing] = \beta_B h_B^2 + \beta_M h_B h_M r_{BM} + \beta_{B(\text{male})} h_B h_{B(\text{male})} r_{G_{BB}} + \beta_{M(\text{male})} h_B h_{M(\text{male})} r_{G_{BM}}$$

where β_X , h_X^2 , r_{XY} , $r_{G_{XX}}$ represent the selection gradient for trait *X*, the heritability of trait *X*, the genetic correlation between traits *X* and *Y* within a single sex, and the between-sex genetic correlation between female *X* and male *X*, respectively (Via, 1984; Roff, 1997; Reeve and Fairbairn, 2001; Charmantier *et al.*, 2006). Unless otherwise noted, all variables in the above equation refer to the female matrix and vector of selection. The trait subscripts represent body size (*B*) and wing morph (*M*). The initial product of the equation ($\beta_B h_B^2$) represents direct selection on female body size, the subsequent product represents the influence of the female correlated character also under selection, and the final two products represent the influence of the male correlated characters under selection. Male body size response to selection, $R_{B[\delta]}$, was also calculated by swapping the female variables for the male variables in the above equation.

Standard deviations for the predicted evolutionary responses were generated via Monte Carlo simulations of the standardized selection gradients and our observed genetic estimates. Normal distributions were created based on the mean and standard deviations of the selection gradient estimates for both males and females. From these distributions, new selection gradients were randomly chosen. These new selection gradients were then applied to the genetic matrices to calculate a new predicted response. This process was repeated 500 times and standard deviations were calculated from these results. All analyses were conducted using SAS version 8.1.

Results

Estimation of selection gradients

Univariate selection gradients (β'_X) suggested that male body size and the long-winged morph were under positive selection ($\beta'_B \pm \text{s.e.}: 0.27 \pm 0.07$; $F_{1,189} = 16.19$, $P < 0.0001$; $\beta'_M \pm \text{s.e.}: 0.19 \pm 0.07$; $F_{1,189} = 7.46$, $P < 0.0069$). Multivariate gradients (β_X) also indicated positive body size selection ($\beta_B \pm \text{s.e.}: 0.23 \pm 0.07$, $F_{1,188} = 10.22$, $P < 0.0016$), however, wing morph selection was not significant ($\beta_M \pm \text{s.e.}: 0.10 \pm 0.07$; $F_{1,188} = 1.78$, $P < 0.1837$). Female univariate selection gradients suggested that body size was under positive selection ($\beta'_B \pm \text{s.e.}: 0.25 \pm 0.08$; $F_{1,278} = 11.33$, $P < 0.0009$), but that wing morph selection was not significant ($\beta'_M \pm \text{s.e.}: -0.05 \pm 0.08$; $F_{1,278} = 0.45$, $P < 0.5030$). Female

Table 1 Genetic parameters

	Female size	Female morphology	Male size	Male morphology
Female size	0.246 ± 0.092 <i>P</i> = 0.0052	-0.528 ± 0.274 <i>P</i> = 0.0602	0.901 ± 0.224 <i>P</i> = 0.0002	-0.437 ± 0.934 <i>P</i> = 0.6421
Female morphology	—	0.611 ± 0.213 <i>P</i> = 0.0031	0.512 ± 0.277 <i>P</i> = 0.0710	0.964 ± 0.555 <i>P</i> = 0.0891
Male size	—	—	0.771 ± 0.267 <i>P</i> = 0.0030	0.414 ± 0.418 <i>P</i> = 0.3271
Male morphology	—	—	—	0.174 ± 0.209 <i>P</i> = 0.4094

multivariate selection gradients showed a similar pattern ($\beta_B \pm \text{s.e.} = 0.28 \pm 0.08$, $F_{1,277} = 13.02$, $P < 0.0004$ vs $\beta_M \pm \text{s.e.} = -0.11 \pm 0.08$; $F_{1,277} = 2.12$, $P < 0.1467$). Although females exhibited a larger magnitude of direct positive selection on size than males, the difference was not significant (*t*-test: $t_{448} = 0.49$, $P = 0.6245$). In contrast, the sexes differed in the direction of selection on the long-winged morph (*t*-test: $t_{448} = -2.06$, $P = 0.0404$).

Estimation of genetic architecture

We found that females were significantly larger than males (femur length mean \pm s.e.: 6.96 ± 0.03 vs 6.62 ± 0.04 mm; $t_{91} = 6.04$, $P < 0.0001$; based on half-sib family least square means). However, the heritability of body size was larger in males than in females (male: $h_B^2 = 0.771 \pm 0.267$; female: $h_B^2 = 0.246 \pm 0.092$; $t_{92} = 1.86$, $P = 0.0662$) and both were significantly different from zero ($P < 0.01$; Table 1). The heritability of wing morphology did not differ significantly between genders (male: $h_M^2 = 0.174 \pm 0.209$; female: $h_M^2 = 0.611 \pm 0.213$; $t_{92} = 1.46$, $P = 0.1465$) and only the female estimate could be bounded away from zero ($P = 0.0031$; Table 1). Interestingly, the within-sex additive genetic correlations between body size and wing morphology had opposite signs in males and females (male: $r_{BM} = 0.414 \pm 0.418$; female: $r_{BM} = -0.528 \pm 0.274$), which were significantly different from each other ($t_{92} = 4.8175$, $P < 0.0001$); genetic correlation were *z*-transformed before comparison; Table 1).

The between-sex additive genetic correlations for body size and wing morph were large and positive ($r_{GBB} = 0.901 \pm 0.224$ and $r_{GMM} = 0.964 \pm 0.555$, respectively; Table 1). Although the between-sex genetic correlation between female body size and male wing morph, as well as between female wing morph and male body size ($r_{GBM} = -0.437$ vs $r_{GMB} = 0.512$, respectively) were not significantly different from zero, they were significantly different from each other ($t_{92} = 4.84$, $P < 0.0001$); genetic correlations were *z*-transformed before comparison; Table 1).

Response to selection

As noted, the evolutionary trajectory of body size may be largely influenced by selection on genetically correlated characters. To examine better how genetic architecture might influence the response to selection, we predicted several different responses by fitting our model in order of increasing complexity. First, we examined male and female response to selection without incorporating the within-sex (r_{BM}) or between-sex genetic correlation

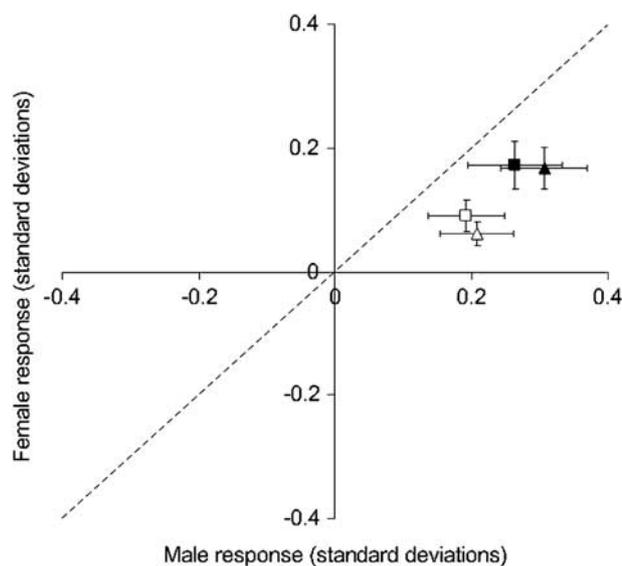


Figure 2 Predictions of next-generation responses to selection. We calculated several selection responses by fitting the model in increasing complexity for both males and females. The simplest model (open triangle) indicated that both male and female body size would increase in the next generation, and that the degree of sexual dimorphism would decrease (below diagonal line). When all of the genetic parameters are considered (closed square), we find that change in the next generation is accelerated significantly by approximately 178% in females (compared to the simplest model) and closer to the line of dimorphic equilibrium, represented by the diagonal. The origin indicates no predicted change. Standard errors around our predictions were based on Monte Carlo simulations. See text for all symbol definitions.

estimates (r_{GBB} , r_{GBM} or r_{GMB}). When only direct selection on size was considered (using the univariate selection gradients), we predicted that size would increase for both sexes and sexual dimorphism would decrease (open triangle, Figure 2). When the within-sex genetic correlations between size and wing morph (open square) were placed into the model, we found that the male response to selection decreased by 8.5% relative to the simplest model, but that the female size response increased by 48%. These data imply that the within-sex genetic correlations can have a strong influence on the evolution of size dimorphism.

Next, we reexamined these two models by including the between-sex genetic correlations (r_{GXX}). We found that all predictions of next-generation change were further from the origin (closed symbols; Figure 2). Again, when body size was examined without wing morph

(closed triangle; Figure 2), we found that the between-sex genetic correlation for body size ($r_{G_{BB}}$) greatly accelerated the male and female response by approximately 50 and 144%, respectively (compared to the simplest model). When all within- and between-sex genetic correlations were included in the analysis (closed square), we predicted a 25% increase in the male response compared to the simplest model (open triangle); although this difference was not significant ($t_{92}=0.64$, $P=0.5243$). Similarly, we found that the female response increased 178% beyond what was predicted by the simplest model (open triangle; $t_{92}=2.65$, $P=0.0094$). Thus, these data imply that the between-sex genetic correlations have a large impact in our predictions of next-generation change in the sexually dimorphic trait.

Discussion

Here we showed that genetic parameters have the potential to produce counterintuitive selection responses in the ground cricket, *A. socius*. When body size alone was examined, our data indicated that future dimorphic evolution should not be restricted, considering that we found ample sex-specific additive genetic variance as well as a between-sex genetic correlation of less than one. Predictions based on these estimates implied that both male and female body size would greatly increase in the next generation, and that sexual dimorphism would decrease (open triangle, Figure 2). When the between-sex genetic correlations for body size ($r_{G_{BB}}$, $r_{G_{BM}}$ and $r_{G_{MB}}$) were included in our model (closed square, Figure 2), we predicted that the response to selection would be greatly accelerated and shift closer to the line of dimorphic equilibrium. Thus, these predictions imply that the underlying sex-specific genetic structure may play a large role in the evolution of sexual dimorphism in the *A. socius* system.

It is important to note that other unmeasured traits may be influencing the evolution of body size in this system. As with any study, the accuracy of our predictions hinge on choosing the appropriate correlated characters, as well as producing appropriate estimates of selection. Although we examined both sexual selection and reproductive selection on body size, we did not examine ecological selection on body size, or dispersal selection on the long-winged morph. It is possible that these selection pressures would modify our estimates of net selective force, and our results should therefore be interpreted with some caution. Regardless of the individual selection estimates, however, we show that the between-sex genetic correlation for a homologous trait (which is not often estimated in either selection or quantitative genetic studies) can play a crucial role in the response to selection.

We also found that macroptery was negatively correlated genetically with body size in females, but positively correlated in males. That is to say, long-winged females were relatively small, whereas long-winged males were relatively large. There are several types of selective environments that could help shape this sizeable difference in genetic architecture. For instance, due to a variety of constraints placed on flight (for example, wing design and flight energetics), there may be a single size optimum (that is, sex-independent)

for dispersal in this system. Moreover, the sexes may possess different fitness optima for body size relative to other reproductive components of fitness. In support of this hypothesis, we found no statistical difference in body size between long-winged females and long-winged males (femur length mean \pm s.e.: 6.90 ± 0.05 vs 6.80 ± 0.05 mm; $t_{69}=1.47$, $P=0.1466$; based on half-sib family least-squares means).

Whenever the optimal expression of a homologous phenotype differs between the sexes (for example, body size), the opportunity for intralocus sexual conflict arises (Rice, 1984; Arnqvist and Rowe, 2005). Intralocus conflict is an interaction between a single gene or gene complex and the sex-specific genetic background, and can have dramatic effects on male and female fitness (Chippindale et al., 2001; Fedorka and Mousseau, 2004). The intensity of this conflict will be to some extent dictated by the strength of the genetic correlation for the homologous character undergoing dimorphic evolution. However, our data suggest that conflict intensity should also be dependent on the magnitude and sign of the genetic correlations of other characters associated with fitness (for example wing morph), since these relationships can either impede or accelerate the rate at which the sex-specific fitness optima are realized. Over time, as these genetic correlations move away from one, each sex will approach their respective fitness optima and intralocus conflict intensity over the dimorphic trait will subside.

Previous work in plants has also helped to elucidate the importance of genetic architecture on future dimorphic evolution (Campbell, 1996; Mitchell et al., 1998; Ashman, 2003; McDaniel, 2005). For instance, Ashman (2005) found that low additive genetic variance and strong genetic correlations for a variety of morphological and phenological characters may act to constrain the evolution of dimorphism between sex morphs in the gynodioecious wild strawberry, *Fragaria virginiana*. Although dimorphism was not the focus of study, antagonistic genetic correlations among traits of the annual legume, *Chamaecrista fasciculata*, were predicted to constrain significantly rates of evolutionary response to selection. Moreover, these predicted rates tended to be much slower than the predicted rates of climate change, suggesting that genetic correlations have the potential to impact future distributions of both flora and fauna in a shifting environment (Etterson and Shaw, 2001).

In summary, our present study indicates that sex-specific genetic parameters may play an important role in the evolution of SSD in *A. socius*. Even though direct selection on body size was similar between the sexes, we predicted that the dimorphic pattern would still be labile. In addition, we found that the between-sex genetic correlations greatly increased our predictions of body size change in the next generation, especially with regard to the female response. Our results have two important implications. First, studies focused on the evolutionary trajectories of traits that are homologous between the sexes may be misleading if a similar male and female genetic structure is assumed. Second, even if a multitude of selective pressures acting on size are known (that is the net selective force), microevolutionary change may still be inaccurately predicted without the accompanying knowledge of the underlying genetic structure.

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