Sex-specific behavioral syndromes allow the independent evolution of behavioral dimorphism

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ABSTRACT

When selection differs by sex, the capacity for sexes to reach optimal phenotypes can be constrained by the shared genome of males and females. Because phenotypic traits are often correlated, this difference extends across multiple traits and underlying genetic correlations can further constrain evolutionary responses. Behaviors are frequently correlated as behavioral syndromes, and these correlations often have a genetic basis. However, whether cross-sex and across behavior correlations lead to constrained evolution remains unknown. Here, we show that a boldness-activity syndrome is strongly sex-specific at the genetic level in the western field cricket (*Gryllus integer*) and that emergence from a shelter is genetically independent between males and females. However, male activity is strongly related to female shelter emergence, creating the potential for biased responses to selection. Our results show that the sex-specific genetic architecture of behavioral syndromes can shape the evolution of behavioral phenotypes.

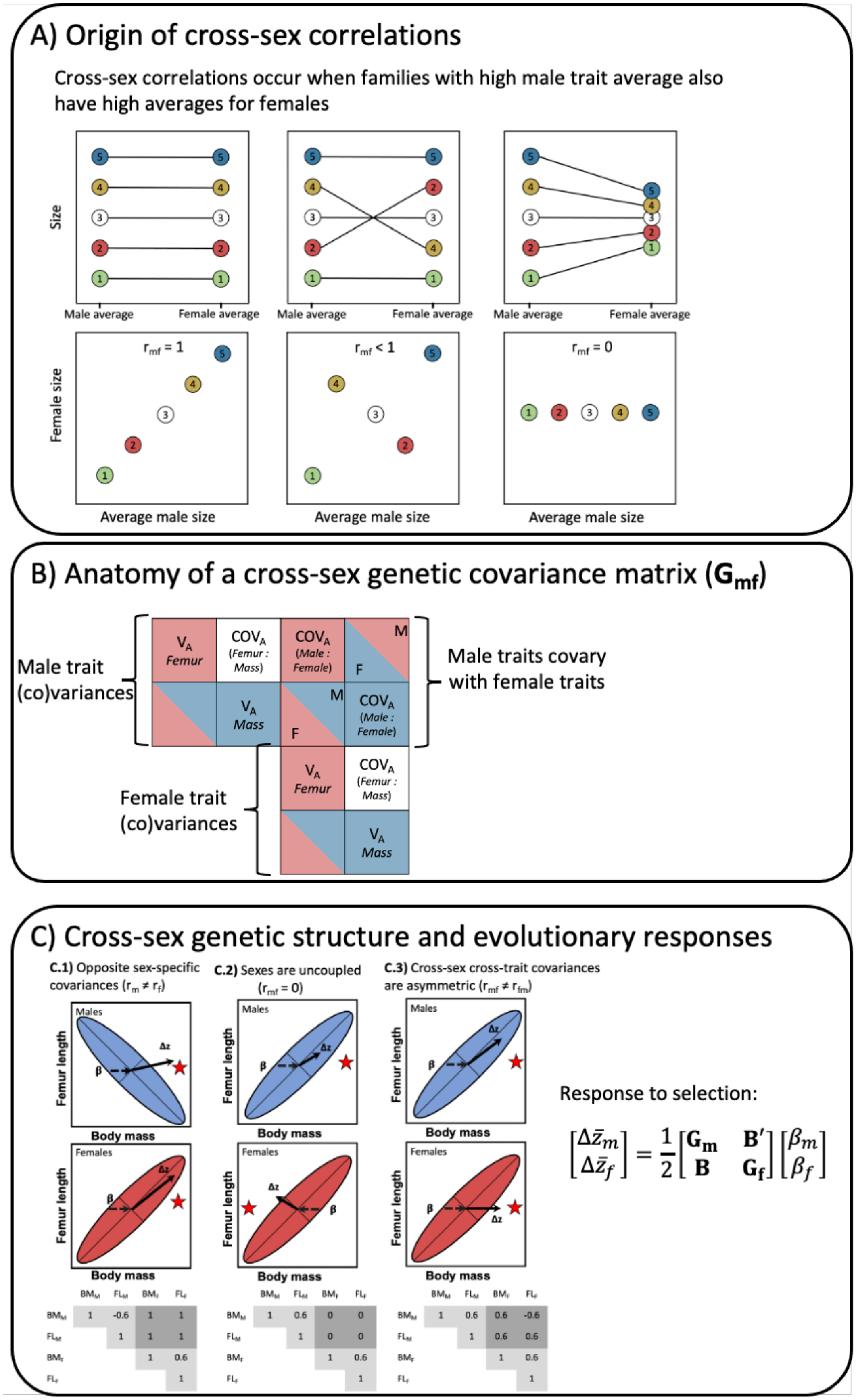
INTRODUCTION

Males and females share the same genome but often rely on different strategies to increase fitness. This can lead to intralocus sexual conflicts where selection acting on a shared trait displaces one sex from its optimum (Hedrick and Temeles 1989; Bonduriansky and Chenoweth 2009). This sexual conflict is further complicated by the constraining potential of genetic correlations(Lande 1980; Walsh and Blows 2009). For example, behaviors are often correlated as components of a behavioral syndrome (Sih et al. 2004) and these behavioral syndromes have the potential to alter evolutionary outcomes (Dochtermann and Dingemanse 2013).

In general, any sustained selection favoring different optima between sexes, i.e. sexually discordant selection, will eventually resolve the sexual conflict and attenuate genetic constraints over time, thus allowing sexes to evolve independently (Delph et al. 2011). This constraint can be formally measured as the cross-sex correlation coefficient r_{mf}, with values < 1 increasing the rapidity at which sexual dimorphism can evolve. Cross-sex correlations are generally large but tend to decrease in species with stronger sexual dimorphism (Poissant et al. 2010). Additional constraints can emerge when generalizing to multiple phenotypes expressed in males and females and their interactions (Lande 1980). By decomposing the additive genetic covariance matrix into its sex-specific ($\mathbf{G_m}$, $\mathbf{G_f}$) and cross-sex sub-matrices (**B**), one can estimate if genetic correlations across sexes and traits create constrained evolutionary outcomes (Fig. 1).

This decomposition approach has been used for morphological traits, revealing that cross-sex covariances (i.e. the **B** matrix, (Lande 1980)) can profoundly alter the evolution of sexual dimorphism (Gosden et al. 2012; Berger et al. 2014; Gosden and Chenoweth 2014), especially when selection favors different average trait values for each sex (Long and Rice 2007; Berger et al. 2014). However, the $\mathbf{G_m}$, $\mathbf{G_f}$, and **B** have rarely been estimated for behaviors. How much the genetic architecture of behavioral syndromes can affect evolutionary outcomes under intralocus sexual conflict remains unclear. This is an important omission because behavior frequently impacts both survival and fitness (Moiron et al. 2020) and sexual dimorphism is common for behaviors (Blanckenhorn 2005; Aragón

2011; Mainwaring et al. 2011; Kokras et al. 2012). Despite many conceptual arguments for why behavioral syndromes should differ by sexes (Schuett et al. 2010; Hämäläinen et al. 2018; Immonen et al. 2018), sex-differences in the expression of behavioral correlations are frequently ignored in practice. As a result, the degree to which cross-sex genetic correlations might be shaped by sexual conflict for behavioral phenotypes remains unknown and the importance of these correlations for the evolution of behaviors is similarly unknown.



A) Origin of cross-sex correlations

Cross-sex correlations occur when families with high male trait average also have high averages for females

B) Anatomy of a cross-sex genetic covariance matrix ($\mathbf{G_{mf}}$)

C) Cross-sex genetic structure and evolutionary responses

C.1) Opposite sex-specific covariances ($r_m \neq r_f$)

C.2) Sexes are uncoupled ($r_{mf} = 0$)

C.3) Cross-sex cross-trait covariances are asymmetric ($r_{mf} \neq r_{fm}$)

Response to selection:

$$\begin{bmatrix}\Delta\bar{z}_m\\ \Delta\bar{z}_f\end{bmatrix} = \frac{1}{2}\begin{bmatrix}\mathbf{G_m} & \mathbf{B'}\\ \mathbf{B} & \mathbf{G_f}\end{bmatrix}\begin{bmatrix}\beta_m\\ \beta_f\end{bmatrix}$$

	BM_M	FL_M	BM_F	FL_F
BM_M	1	-0.6	1	1
FL_M		1	1	1
BM_F			1	0.6
FL_F				1

	BM_M	FL_M	BM_F	FL_F
BM_M	1	0.6	0	0
FL_M		1	0	0
BM_F			1	0.6
FL_F				1

	BM_M	FL_M	BM_F	FL_F
BM_M	1	0.6	0.6	-0.6
FL_M		1	0.6	0.6
BM_F			1	0.6
FL_F				1

Figure 1. The genetic architecture of cross-sex correlations can have non-intuitive consequences on evolutionary responses and sexual dimorphism. A) High values of cross-sex correlations for the same traits (here, body size) indicate that male and female averages are positively correlated among families. B) The cross-sex covariance matrix ($\mathbf{G_{mf}}$) allows to compare patterns of genetic covariances within sexes (here between body mass and body size) as well as understand the strength of cross-trait correlations within and among traits. C) Cross-sex cross-trait correlation (r_{mf}) can produce non-intuitive responses to selective pressures. Here we show 3 scenarios indicative of the variety of responses to selection (Δz) that can occur depending on the direction of selection ($\boldsymbol{\beta}$) and the magnitude and orientation of r_{mf}. The ellipses represent the bivariate (co)variation in femur length and mass, with the population average at the vertex of the (thin solid) lines indicating the directions in bivariate space with the most variation. Dashed lines represent the direction selection ($\boldsymbol{\beta}$) is pushing a population's average and the solid thick arrows show the direction and magnitude (arrow tip) of selection responses. In both scenarios C.1 and C.2, selection is concordant—i.e. acting the same—between sexes and males and females have the same fitness optimum. In scenario C.3, selection is sexually discordant and favors increased sexual dimorphism. Scenario C.1 shows that strong cross-sex cross trait correlations can bias sexes away from their optimum. In scenario C.2, null r_{mf} results in independent trajectories by sexes. In scenario C.3, the effect of fathers on their daughters' phenotype is opposite of that of mother's on their sons', resulting in asymmetric r_{mf} and biased responses to selection in males.

Intralocus sexual conflict should be particularly strong in the field crickets (Gryllidae). In many field crickets, males and females differ in their behaviors and reproductive strategies (Hedrick and Kortet 2012). For example, females explore their environments to sample mates while males remain at burrows from which they signal (French and Cade 1987). Further, a boldness-activity syndrome has a conserved genetic basis in at least one species, the Western stutter-trilling field cricket (*Gryllus integer*), which seems to have constrained behavioral divergence (Royauté et al. 2020). Whether this syndrome is sex-specific is currently unknown but the combination of conserved syndromes together with a lack of sex-specificity would further constrain the ability of populations to respond to local selective pressures.

Here we used behavioral measurements of over 960 *Gryllus integer* individuals to estimate the influence of cross-sex genetic correlations on evolutionary responses. We predicted that crickets would exhibit dimorphism in average activity given the mate-sampling behavior of females and that genetic variance for this trait would be lower for female crickets due to selection favoring increased traveling. We also predicted sex-specificity in the behavioral syndrome, with a stronger positive genetic correlation between antipredator response and activity in females. Since exit from refugia and activity should have a stronger influence on female fitness, we also expected a stronger correlation between shelter emergence with activity and antipredator response in females. Although there are few estimates for cross-sex correlations of behaviors, those available suggest behaviors are under similar constraints as other phenotypes (Poissant et al. 2010). We therefore expected that cross-sex genetic correlations (r_{mf}) would not depart significantly from 1. We tested these predictions by estimating the cross-sex covariance matrix, i.e. $\mathbf{G_{mf}}$, decomposed into its sex-specific and cross-sex sub-matrices ($\mathbf{G_m}$, $\mathbf{G_f}$ and $\mathbf{B}$ submatrices, Figure 1). We compared the strength of covariances among sexes and the effects of these covariances on responses to selection using random skewer analysis.

METHODS

We collected adult female crickets from four populations throughout the southwestern and western US: Socorro, NM; Las Cruces, NM; Aguila, AZ; and Dunnigan, CA (Figure 2) during the summer of 2017 and housed them and in our laboratory facilities at North Dakota State University. Females were housed individually in 0.71 L containers and provided with ad libitum food (Purina Chick Starter) and water (water was provided in glass vials capped with cotton). Each cricket was also provided with a small piece of cardboard egg carton for shelter. The cricket housing room was maintained ~27C on a 12:12 dark:light cycle reversed such that the room was dark during daytime hours. We run offspring of this parental generation through multiple behavioral trials before mating individuals at random within each population. We repeated this process for two additional generations.

Behavioral testing

Latency to emerge from shelter

Gryllid crickets use small burrows and natural cracks as refuges to which they retreat when under threat. The time taken to emerge from a shelter after disturbance can therefore be considered a proxy for risk-taking behavior or "boldness" (Kortet and Hedrick 2007). We transferred individuals from their home containers into small artificial burrows (40 cm^3) placed within a 34.6 × 21 cm arena. We left the crickets to rest for two minutes after which we removed the cap from the burrow and let individuals emerge. We then recorded how long it took for an individual to emerge (in seconds) for up to six minutes and thirty seconds. Individuals that did not emerge were given a maximum latency of 390 seconds.

Open field exploratory behavior

We used open field tests to measure activity and exploratory propensity in a 30 × 30 cm plexiglass arena. These tests are classic behavioral assay across taxa (Walsh and Cummins 1976) and can reveal strong among-individual differences in exploration patterns, including in crickets (Royauté et al. 2015, 2019; Royauté and Dochtermann 2017). Individuals that move through more of the arena are considered more thorough explorers (Réale et al. 2007). We introduced individuals into the arena and left them to rest under a small container for 30 seconds. At the end of this 30 seconds, we removed the container and the cricket was allowed to explore the arena for 3 minutes and 40 seconds. The arena was cleaned with isopropyl alcohol between trials to remove any chemosensory cues from the arena. We used Ethovision XT to record the total distance the individual moved during the trial (cm).

Response to cues of predator presence

We measured the response to cues of predator presence, a behavioral assay commonly used in Gryllid species to determine antipredator response (Royauté and Dochtermann 2017; Royauté et al. 2019). Specifically, individuals were introduced into a 15 cm diameter circular arena (7.5 cm height), the floor of which was covered with dry filter paper that had been soaked with diluted excreta from leopard geckos (*Eublepharis macularius*). Crickets respond to exposure to leopard gecko cues by increasing activity and individuals with higher distance moved are considered more responsive to the cue (Royauté and Dochtermann 2017; Royauté et al. 2019). We introduced crickets to a portion of the arena without predator cue and left them to rest under a small shelter for 30 seconds. We then removed the shelter and allowed the individual allowed to freely move throughout the arena for 3 minutes and 40 seconds. We then used Ethovision XT to record the total distance an individual moved during the trial (cm).

Statistical analyses

All analyses were performed using R version 4.0.3 (R citation) using the MCMCglmm package (Hadfield 2010).

Estimation of cross-sex genetic covariances ($\mathbf{G}_{\mathbf{mf}}$*)*

We used a multi-response mixed effect animal models (Kruuk 2004; Wilson et al. 2010) to estimate genetic variances and covariances (i.e. the $\mathbf{G}_{\mathbf{mf}}$ matrix). We included the effects of temperature, day and time of testing in the behavioral arena room along with sex, life-stage and mass of the individual as fixed effects. We used the individual relatedness matrix (based on the known pedigree) as a random effect and the following behavioral traits were included as response variables: (i) the latency that an individual emerged from the shelter during the trial (modeled as censored Gaussian), (ii) the distance moved during the open field trial (Gaussian), (iii) the distance an individual moved during the predator cue response trial (Gaussian). To estimate both sex-specific and cross-sex covariances, we treated the behavior of each sex as a separate trait - resulting in the estimation of a 6×6 covariance matrix. We ran the multi-response model with an MCMC chain of 4.8×10^6 iterations, with an 800,000 burn-in period and a thinning interval of 4,000 and we used a parameter expanded prior that was minimally informative for both variances and covariances. All variances and covariances were estimated at the additive genetic level and on the latent scale.

Estimation of behavioral dimorphism

We tested for the existence of sexual dimorphism in behavioral expression by comparing linear coefficient for the sex fixed effect included in our multivariate animal model and base our statistical inference on their Bayesian probability (Pmcmc). This metric varies between 0.5 and 1 and indicates the probability of a significant difference based on the number of posterior estimates overlapping with 0. Pmcmc values > 0.95 were judged as significant.

Comparison of sex-specific covariances ($\mathbf{G_m}$ and $\mathbf{G_f}$ matrices)

We used a two-step approach to compare the intensity of the difference in genetic covariances among sexes. First, we calculated the difference in covariance between males and females (Δ COV_A) for each pair of behaviors and their associated Bayesian probabilities (Pmcmc). Next, we tested whether sex-specific covariances were similarly oriented. To do so, we calculated the vector correlation ($r°$) between axes containing the highest amount of genetic variation using eigenvalue decomposition. We then estimated whether the resulting vector correlations among eigenvectors of **G** differed substantially from expectations of 0 (no alignment of genetic variation among sexes) and 1 (perfect alignment). Because vector correlations are bounded by 0 and 1, we estimated the Region of Posterior Equivalence (ROPE) which we defined as the intervals [0.0; 0.1] and [0.9; 1.0]. Estimates falling within these ROPE regions are judged “practically equivalent” to vector correlations of 0 and 1 respectively. We converted the proportion of estimates falling outside these ROPE regions into Pmcmc values to infer significance, with Pmcmc > 0.95 indicating significant departure from these null hypotheses.

*Estimating the genetic constraint imposed by the cross-sex covariance matrix (**B**)*

We first tested whether cross-sex covariances within traits differed significantly from 0 and 1. Cross-sex covariances are represented on the diagonal elements of the **B** matrix. A covariance of 0 indicate complete genetic independence among sexes, which we determined using Bayesian probabilities (Pmcmc). To test for a departure from complete genetic coupling among sexes, we converted the covariances to correlation coefficients (r_{mf}) and used the ROPE test described above. We then investigated whether cross-sex cross-traits covariances – represented on the off-diagonal elements of **B** – differed significantly from one another by calculating the posterior difference in covariance as described (Δ COV_A).

Next, we compared the evolutionary trajectories of sexes with a scenario were sexes evolved independently with one were sexes were fully constrained (Cox et al. 2017). To do so, we simulated 500 selection gradients based on a multivariate normal distribution that we scaled to unit length. We generated concordant selection gradients by assigning the same values to male and female gradients ($\beta_f = \beta_m$) and discordant selection by setting $\beta_f = -\beta_m$. We applied each selection gradient to all 1,000 posterior covariance matrices of $\mathbf{G_{mf}}$ estimated from our multivariate animal model, thus ensuring we took the uncertainty in estimates forward. We then calculated the resulting response to selection ($\Delta\bar{z}$) by applying the multivariate breeder’s equation for cross-sex covariance (Lande 1980):

$$\begin{bmatrix} \Delta\bar{z}_f \\ \Delta\bar{z}_m \end{bmatrix} = \frac{1}{2}\begin{bmatrix} \mathbf{G_f} & \mathbf{B}' \\ \mathbf{B} & \mathbf{G_m} \end{bmatrix}\begin{bmatrix} \beta_f \\ \beta_m \end{bmatrix} \quad \text{(equation 1)}$$

We contrasted these responses to selection to cases where we set all cross-sex covariances 0 and by fully constraining cross-sex correlations to 1. To achieve this last step, we converted $\mathbf{G}_{\mathbf{mf}}$ to a correlation matrix and replaced **B** elements by 1. We then back-converted this modified matrix into covariances by replacing the diagonal elements of **B** by the geometric mean of male and female genetic variances (i.e. the diagonal elements of $\mathbf{G}_{\mathbf{f}}$ and $\mathbf{G}_{\mathbf{m}}$ respectively). We then estimated the vector correlation between the response calculated from our estimated matrix and those estimated with unconstrained ($r_{B = 0}$) and constrained matrices ($r_{B = 1}$). Next, we compared how consistent male and female response was when evolving toward the same optimum (concordant selection) and when selection was discordant. This was achieved by calculating the vector correlation between the direction of selection for each sex and the corresponding response ($r_{\beta\times\Delta z}$).

RESULTS

Males and females showed little evidence for sexual dimorphism in average behavior (all Pmcmc < 0.57, Table S1, S2). We did find evidence of a **G** × **Sex** interaction, and females had lower heritability and evolvability compared to males (mean female $h^2 = 0.10$; mean male $h^2 = 0.47$; mean female $I = 3.04$ %; mean male $I = 15.73$ %). This is confirmed by the fact that the additive genetic variance was lower in females compared to males for all three behaviors (posterior median [89 % CI]; shelter emergence: $\Delta V_{A\,(\text{females – males})} = -50.12$ [-110.18; 8.18], Pmcmc = 0.92; activity: $\Delta V_A = -43.38$ [-89.01; -9.19], Pmcmc = 0.99; antipredator response: $\Delta V_A = -17.63$ [-44.47; 5.45], Pmcmc = 0.92) (Figure 2, 3; Table S3).

We also found strong evidence for the sex-specific expression of behavioral syndromes, with weaker genetic correlations between behaviors in females. Males and females differed primarily in how shelter emergence related to open-field activity and antipredator response (Figure 2), while the relationship between open-field activity and antipredator response was stable between sexes (females: $r_{mf} = 0.65$ [0.20; 0.98], Pmcmc = 0.94, Pmcmc = 0.91; males: $r_{mf} = 0.64$ [0.27; 0.92], Pmcmc = 0.98). Females that stayed longer in the shelter had lower antipredator response and travelled further in the open-field (shelter emergence × open-field: $r_{mf} = -0.45$ [-0.92; 0.11], Pmcmc = 0.86; shelter emergence × antipred. : $r_{mf} = -0.48$ [-0.90; -0.01], Pmcmc = 0.91). In contrast, males with slow shelter emergence had higher activity and antipredator response (shelter emergence × open-field: $r_{mf} = 0.47$ [0.06; 0.87], Pmcmc = 0.93; shelter emergence × antipred. : r_{mf} = 0.50 [-0.01; 0.84], Pmcmc = 0.92). In addition, the correlation between major axes of genetic variation ($\mathbf{g}_{\mathbf{max}}$) was significantly < 1, providing another line of evidence for the presence of a sex-specific syndrome (vector correlation r° = 0.36 [0.00; 0.76], $\mathrm{Pmcmc}_{\neq 1}$ = 0.97) (Table S2, S3).

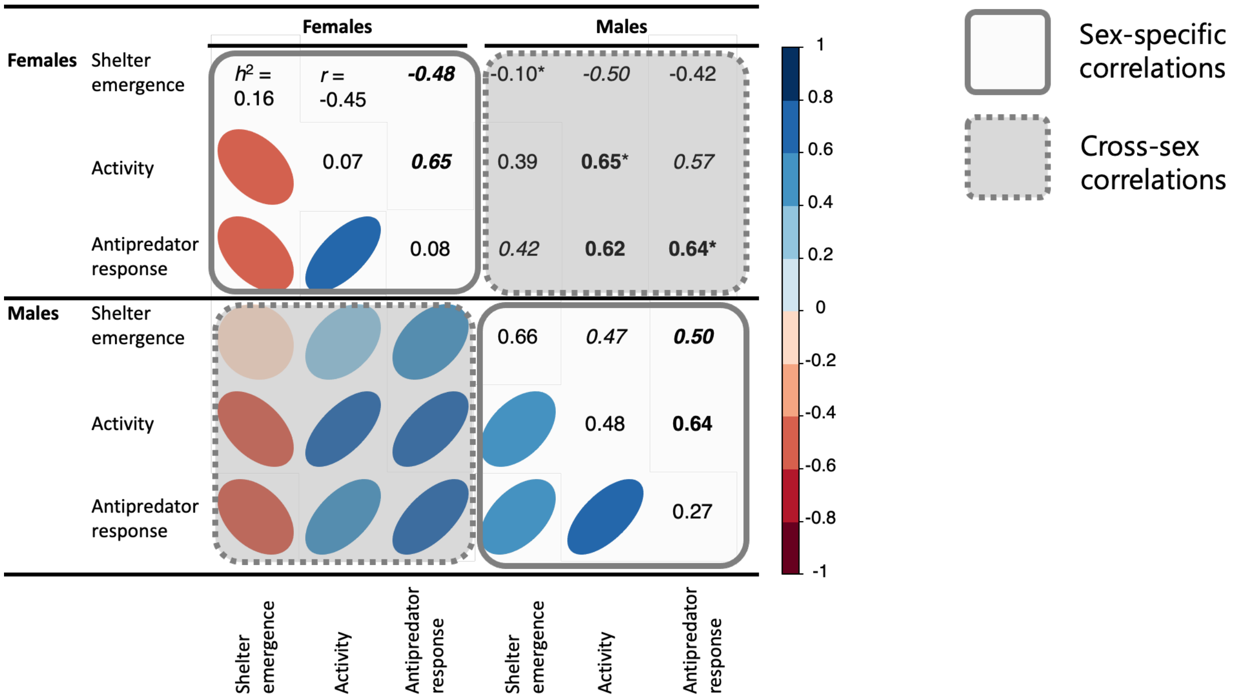


Figure 2. Genetic correlation matrix ($\mathbf{G}_{\mathbf{mf}}$) indicating sex-specific and cross-sex genetic correlations. Heritabilities (h^2) are indicated on the main diagonal and genetic correlations (r) on the off-diagonal elements. Off-diagonal elements represent either the sex-specific genetic correlations (r_f and r_m in light grey) or the cross-sex genetic correlations (r_{mf} in dark grey). Bold indicate significant correlations based on Pmcmc > 0.95. Correlations with Pmcmc > 0.90 are indicated in italics. Cross-sex correlations significantly different from 1 are indicated with an asterisk.

All behaviors showed weak to moderate cross-sex correlations and were significantly below 1 (shelter emergence: r_{mf} = -0.09 [-0.59; 0.39], $Pmcmc_{\neq 1}$ = 1.00; activity: r_{mf} = 0.65 [0.22, 0.97], $Pmcmc_{\neq 1}$ = 0.94; antipredator response: r_{mf} = 0.64 [0.26; 0.94], $Pmcmc_{\neq 1}$ = 0.96) (Table S3). In addition, sexes had biased expression of different trait combinations, as indicated by the high proportion of asymmetry in **B—**the cross-sex covariance matrix (proportion of skew-symmetry = 0.25 [0.04, 0.42]). This degree of asymmetry was most pronounced for the cross-sex correlations between shelter emergence and activity (ΔCOV_A = -21.39 [-43.72; -0.56], Pmcmc = 0.97) and between shelter emergence and antipredator response (ΔCOV_A = -14.8 [-32.33; 1.46], Pmcmc = 0.95). In contrast, the correlation between activity and antipredator response did not differ among sexes (ΔCOV_A = -3.02 [-11.73; 6.73], Pmcmc = 0.71) (Figure 3).

This means that highly active fathers produced daughters with faster shelter emergence (r_{mf} = -0.50 [-0.85; -0.06], Pmcmc = 0.94) and higher antipredator response (r_{mf} = 0.57 [0.12; 0.95], Pmcmc = 0.93). In contrast, active mothers only weakly contributed to their sons' shelter emergence (r_{mf} = 0.39 [-0.14; 0.85], Pmcmc = 0.85) and antipredator response (r_{mf} = 0.42 [-0.01; 0.85], Pmcmc = 0.90).

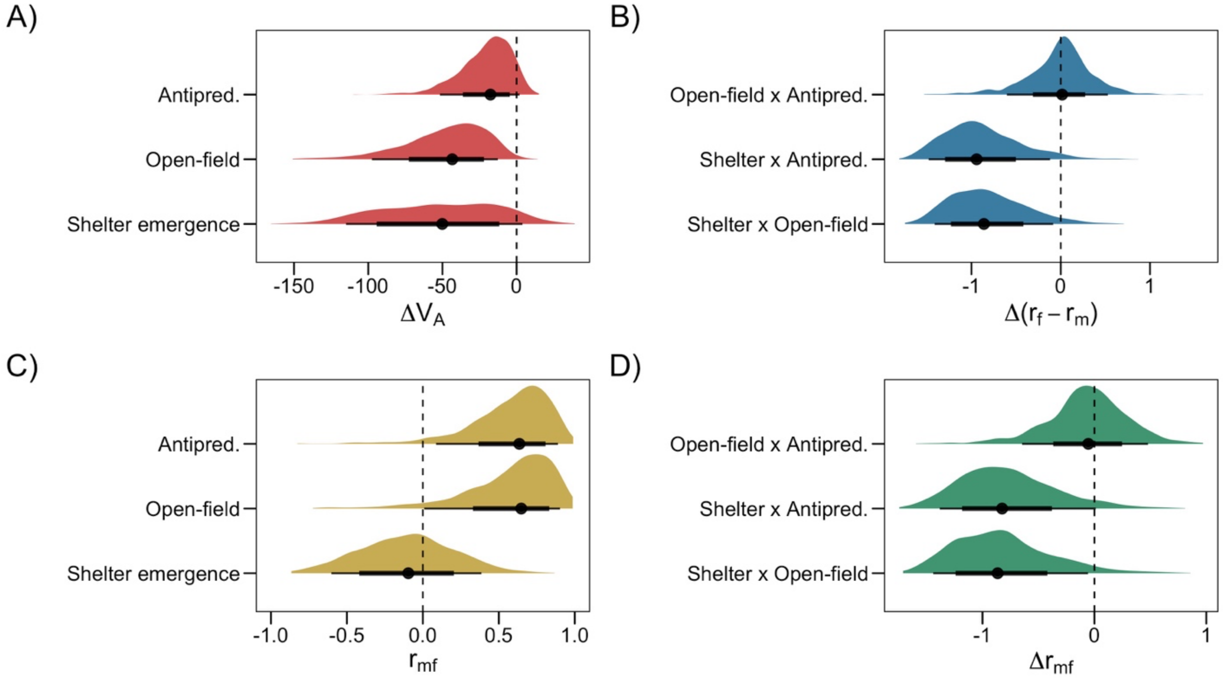


Figure 3. The genetic structure of the boldness-activity syndrome differed both in terms of its sex-specific genetic variances (A) and correlations (B) as well as its cross-sex correlations within traits (C) and cross-sex cross-traits correlations (D).

Finally, by simulating responses to selection, we found that evolutionary trajectories were more consistent with behaviors being sexually independent than with a constrained expression of behaviors. This was the case regardless of whether selection favored sex-specific optima (i.e. discordant selection: $r_{B=0}$ = 0.95 [0.73; 1.00]; $r_{B=1}$ = 0.28 [0.00; 0.56]; Δr = 0.64 [0.24; 0.98], Pmcmc = 0.96) or when both sexes had the same optimum (i.e. concordant selection: $r_{B=0}$ = 0.95 [0.74; 1.00], Δr = 0.23 [-0.04; 0.66], Pmcmc = 0.95) (Figure 4). We next compared the agreement between simulated selection gradients and predicted response to selection ($r_{\beta \times \Delta z}$) between sexes. Males and females had equally consistent responses to concordant selection (female $r_{\beta \times \Delta z}$ = 0.72 [0.29; 1.00]; male $r_{\beta \times \Delta z}$ = 0.75 [0.47; 1.00]; $\Delta r_{\beta \times \Delta z}$ = -0.19 [-0.67; 0.07], Pmcmc = 0.88). However, female response tended to be biased away from selection compared to males when selection was discordant (female $r_{\beta \times \Delta z}$ = 0.50 [0.06; 0.95]; male $r_{\beta \times \Delta z}$ = 0.77 [0.46; 1.00], $\Delta r_{\beta \times \Delta z}$ = -0.27 [-0.75; 0.11], Pmcmc = 0.86). This could mean that the magnitude of the genetic constraint is expressed more strongly in males, which is consistent with the asymmetric nature of the cross-sex covariance matrix. However, this last result should be interpreted with caution given the wide credible intervals around these estimates.

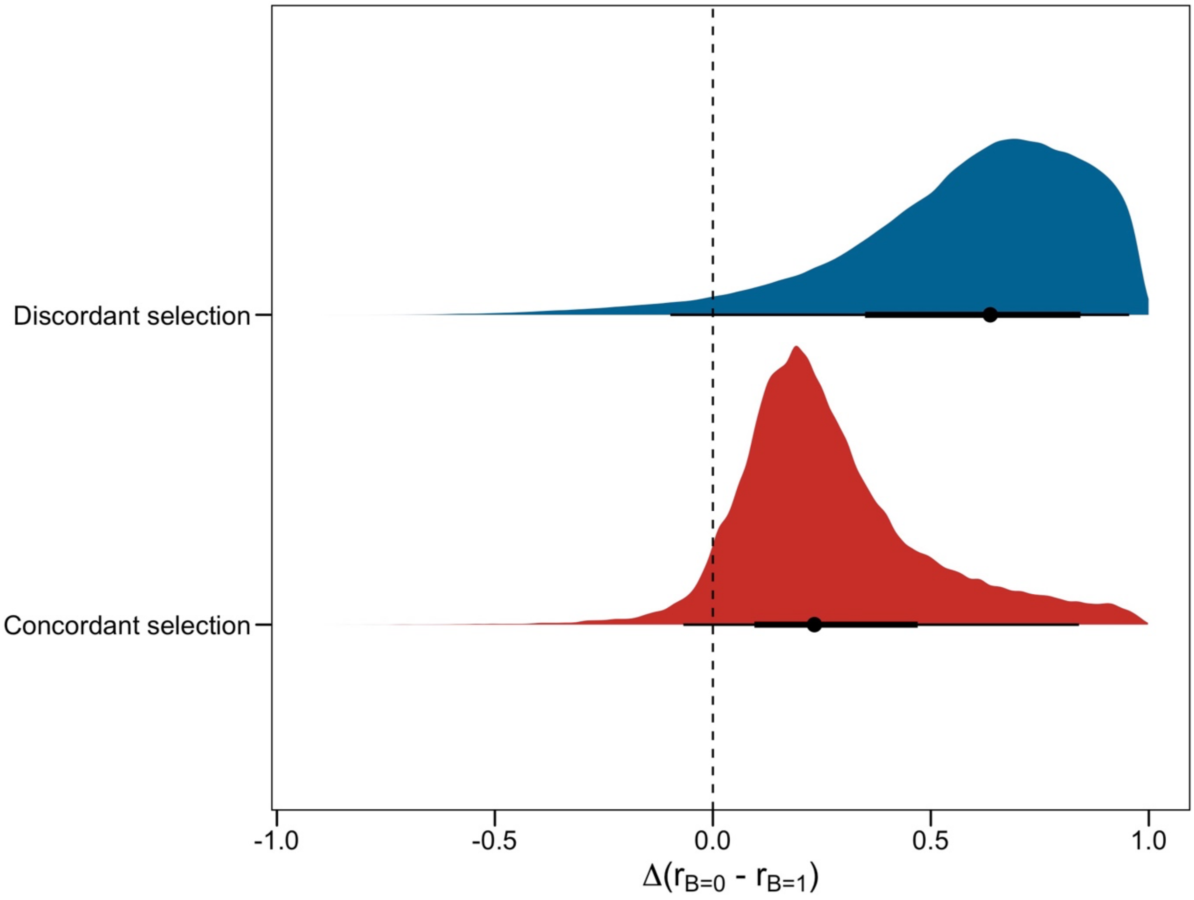


Figure 4. The response to selection is more consistent with models were sexes evolve independently (**B** = 0) than models where sexes are fully constrained (**B** = 1). This trend is most pronounced when selection favours opposite optima among sexes (discordant selection). Positive values indicate that the observed response to selection (Δz) is more strongly correlated with responses to selection where elements of the cross-sex covariance matrix are set to 0 (**B** = 0) compared to responses to selection where the cross-sex covariance is fully constrained (**B** = 1), based on 1,000 random selection gradients applied to each 1,000 posterior covariance matrices.

DISCUSSION

Our results show that males and females differ substantially in their behavioral syndromes at the genetic level. Shelter emergence was genetically independent between males and females, whereas the genetic constraint for activity and antipredator response was stronger but still departed from 1. The absence of a strong genetic constraint linking the sexes is surprising given that the behaviors we measured are not typically considered distinct sex-specific traits. In the case of shelter emergence, a cross-sex correlation approaching zero implies that the same behavior is underpinned by completely independent sets of genes in males and females. Such genetic uncoupling means that this behavior can fulfill different functions in each sex and can evolve independently. Our results suggest that sexual conflict may have been resolved in this species even in absence of observable behavioral dimorphism.

By applying a quantitative genetic approach, we were able to uncover multiple ways in which sexes differed in their behaviors. While males and females did not differ in mean behaviors, we uncovered a signature of behavioral dimorphism in the amount of genetic variation expressed by each sex. This **G** × **Sex** effect was characterized by female behavior being less heritable than observed for males. In our case, traits with lower heritabilities also had lower evolvabilities, indicating that females are less responsive to selective pressures than males in this species. This strong difference in genetic variance between sexes could result from stronger stabilizing selection in females eroding genetic variation in traits related to exploration and risk taking while maintaining a similar optimum in each sex. Multivariate stabilizing selection has indeed been shown to be an important driver of trait evolution, for example in genital morphology in arthropods (Arnqvist 1997; House et al. 2020). Another possibility is that rearing individuals in laboratory conditions with ad-lib access to food and shelter could alleviate the resource acquisition and allocation trade-offs that may be negotiated differently by each sex. This explanation is especially plausible if males and females modify their phenotypes to different degree in response to captivity. Note too that the environmental contribution to females' behavioral phenotype was much greater than that of males, leaving space for differential adjustment of behavior by sexes to occur.

Males and females differed substantially in how they expressed a boldness-activity syndrome. Contrary to our predictions, in both sexes active genotypes were also more sensitive to predatory cues, with no change to the magnitude of the genetic correlation. The primary difference was therefore in how shelter emergence related to activity and antipredator response. “Bold” females – i.e. females with fast emergence from the shelter – had higher activity and antipredator response. In contrast, active males were more sensitive to predator cues and behaved cautiously when emerging from the shelter. This result provides important insight into how male and female crickets handle risky situations. Female must travel through risky environments in order to locate mates. Therefore, bold and active genotypes may need to compensate for these risky behaviors by being more reactive to the presence of predator cues. Males, in contrast, stay close to their shelter but produce courtship signals that make them the target of predators and parasites. As a result, bolder males may ignore the presence of predatory cues if this strategy yields higher frequency of encounters with females. This type of risk compensation strategy has already been shown in previous studies where males with more attractive songs stay longer in shelters (Hedrick 2000).

Our findings that males and females differed in the genetic expression behavioral syndromes and that cross-sex correlations are uncoupled suggest that risk-taking is regulated by different physiological pathways in each sex. In crickets, several monoamine neurohormones are involved in the regulation of multiple behaviors tied to a “fight or flight” response, including aggression, courtship, dispersal and response to simulated predation exposure (Adamo et al. 1995, 2013; Stevenson and Rillich 2016; Adamo 2017; Lundgren et al. 2021). However, experiments tend to either focus on males exclusively or are not designed to address sex-differences in physiological mechanisms. However, sex-differences in a similar axis of variation, the proactive/reactive axis, have also been described in several vertebrate taxa (Kokras et al. 2012; Immonen et al. 2018).

The genetic structure of behavioral syndromes is highly conserved in this species, even across isolated populations (Royauté et al. 2020). This indicates that behavioral syndromes may not vary much when exposed to different selective pressures. Instead, genetic constraints resulting from pleiotropy was the more likely explanations for the presence of behavioral syndrome in this species. Here, we show that behavioral syndromes differed more strongly between sexes than among populations. A likely explanation is that males and females express sex-specific behaviors regardless of the population of origin. As a result, selection may be more likely to differ between sexes than between populations. While comparisons of differences in selection among sexes and populations are scarce, previous studies suggest that sexually discordant selection is common in the wild and tends to be stronger in traits in which sexual dimorphism is pronounced (Cox et al. 2009).

While rarely investigated, sex specific differences in behavioral syndromes have been demonstrated in some species. However, most of these studies have focused on comparisons of behavioral repeatabilities between males and females in single traits (Jenkins 2011; Debeffe et al. 2015) rather providing a broader exploration of multivariate patterns of cross-sex correlation in behavioral traits, as we did here. Interestingly, (Hedrick and Kortet 2012) previously identified sex differences in the repeatability of shelter emergence in a separate population of *G. integer*. Contrary to what we detected, males had lower repeatability compared to females. Note that repeatability and heritability are not directly comparable because repeatability also includes sources of variation due to the "permanent environment" while heritability only includes additive genetic variation. More recently several studies have also compared syndrome structure among sexes with mixed results. Some studies reported large differences in behavioral syndromes between males and females (Fresneau et al. 2014; Han et al. 2015; Royauté 2015; Way et al. 2015) while others support a conserved syndrome structure between sexes (Michelangeli et al. 2016; Goulet et al. 2021). Our results supply an additional line of evidence in favor of sex-specific syndromes.

There is only limited exploration of multivariate patterns of cross-sex correlation in behavioral traits. Most studies reported from (Poissant et al. 2010) concern single traits and point to strong cross-sex correlations with relatively weak dimorphism for behavior. The majority of these estimates were, however, from studies interested in sexual selection, with < 4 % of estimates coming from explicitly behavioral studies. Because we also estimated the cross-sex correlation at the additive genetic level, we were able to determine that behavioral traits may be less constrained by sex than previously thought. Indeed, our mean estimate for r_{mf} was much weaker than observed in previous studies evaluating intra-locus sexual conflicts in behavior (mean rmf = 0.46 vs. 0.77, Poissant et al. 2010). Our results suggest that behavioral traits may commonly fulfill different functions between sexes and should therefore be analyzed as separate traits between the sexes in behavioral syndrome and animal personality studies.

Very few studies have been able to estimate the genetic contribution of sexes to behavioral syndromes as we have done here. In the orb-weaving spider *Nuctenea umbratical*, cross-sex correlations for activity and aggression were in the same range as our estimates for activity and antipredator response ($r_{mf} = 0.50$) (Kralj-Fišer et al. 2019). In *Gryllus bimaculatus*, which is closely related to *G. integer*, exploration and aggression are more strongly correlated in females and these traits have asymmetric contributions across sexes (Han et al. 2019). However, cross-sex correlations within traits were qualitatively stronger than observed in our study (mean $r_{mf} = 0.70$ vs mean $r_{mf} = 0.46$), pointing to a stronger genetic constraint between sexes than we observed in *Gryllus integer*. Finally, White et al. (2019) showed differences between sex-specific covariances in guppies to similar *G. integer*. However, they reported a much weaker signal of asymmetry in **B**. The fact that these few studies differ widely in conclusions shows that there is no consensus yet on how behavioral syndromes differ between sexes and even closely related species may show strong differences in the expression of behavioral dimorphism.

Other studies, conducted primarily on morphological traits, point to strong constraints imposed by genetic cross-sex covariances (Gosden et al. 2012; Gosden and Chenoweth 2014; Sztepanacz and Houle 2019). In our case, the constraining effect of cross-sex covariances was weak at best and responses to selection were more consistent with independent evolutionary trajectories for each sex. This is similar to a previous study on sexually dimorphic ornaments in brown anoles which showed that the cross-sex covariance among ornaments did not substantially constrain the evolution of dimorphism (Cox et al. 2017).

We found a high degree of asymmetry in the cross-sex cross-traits components of the genetic covariance matrix. In particular, male activity had a stronger contribution to female shelter emergence than female activity on male shelter emergence. This type of asymmetric contribution to the phenotype is expected to bias responses away from selection. In *Drosophila* for example, wing shape evolution is primarily shaped by cross-sex covariances for the same trait (i.e. the diagonal elements of **B**) rather than cross-sex cross-trait covariances (Sztepanacz and Houle 2019). This was the case even though upper and lower elements of the **B** matrix frequently had opposite signs and despite a general, though weaker, signal of asymmetry such as we report here (5 % vs. 25 %). Despite strong asymmetry in our estimate of cross-sex covariances, we found only weak evidence for biased responses to selection. Instead, our simulations of the responses to selections showed that the evolution of behavioral dimorphisms was more consistent with scenarios in which sexes are genetically uncoupled and allowed to evolve independently compared to a fully constrained cross-sex genetic architecture. This means that the independent evolutionary trajectories by sexes we report are likely a result of the weak cross-sex correlations within traits we detected (mean $r_{mf} < 0.50$).

We show that traits involved in studies of animal personality have a sex-specific genetic architecture. These behaviors are genetically uncoupled between sexes and allow sexes to follow independent evolutionary trajectories. Our results are intriguing because theory predicts that cross-sex covariances will act as constraints and limit the abilities of sexes to reach their optimum. The type of genetic independence we found suggests a past history of discordant selection that has strongly shaped behavioral dimorphism and has resolved sexual conflict in this species.

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