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Cross-sex genetic correlation does not extend to sexual size dimorphism in spiders

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Abstract

Males and females are often subjected to different selection pressures for homologous traits, resulting in sex-specific optima. Because organismal attributes usually share their genetic architectures, sex-specific selection may lead to intralocus sexual conflict. Evolution of sexual dimorphism may resolve this conflict, depending on the degree of cross-sex genetic correlation (r_{MF}) and the strength of sex-specific selection. In theory, high r_{MF} implies that sexes largely share the genetic base for a given trait and are consequently sexually monomorphic, while low r_{MF} indicates a sex-specific genetic base and sexual dimorphism. Here, we broadly test this hypothesis on three spider species with varying degrees of female-biased sexual size dimorphism, *Larinioides sclopetarius* (sexual dimorphism index, SDI = 0.85), *Nuctenea umbratica* (SDI = 0.60), and *Zygiella x-notata* (SDI = 0.46). We assess r_{MF} via same-sex and opposite-sex heritability estimates. We find moderate body mass heritability but no obvious patterns in sex-specific heritability. Against the prediction, the degree of sexual size dimorphism is unrelated to the relative strength of same-sex versus opposite-sex heritability. Our results do not support the hypothesis that sexual size dimorphism is negatively associated with r_{MF}. We conclude that sex-specific genetic architecture may not be necessary for the evolution of a sexually dimorphic trait.

Keywords Cross-sex genetic correlation · Trait evolution · Sexual dimorphism · Heritability · Sex-specific optimum · Pedigree

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Introduction

In most sexual organisms, both genders usually share the same genetic architecture for homologous traits (Lande 1980). When selection pressures on those traits are different in males and females, sex-specific trait optima may arise. In extreme cases, sex-specific selection acts in opposite ways, setting a stage for intralocus sexual conflict. If unresolved, this conflict prevents the sexes from achieving their respective trait optima, resulting in sex-specific fitness reductions (Pennell and Morrow 2013). Evolution of sexual dimorphism (SD) may fully or partially resolve sexual conflict, depending on the degree of cross-sex genetic correlation (r_{MF}) for the trait and the strength of sex-specific selection (Lande 1980). Theoretically, high r_{MF} should constrain the evolution of SD and sustain sexual conflict. In other words, if r_{MF} equals 1, males and females are monomorphic due to near identical genetic architecture for the trait. If, on the other hand, r_{MF} is close to zero, this would imply a sex-specific genetic base, allowing for SD.

This scenario can be studied using trait heritability analysis. r_{MF} can be expressed as

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$$r_{MF} = \sqrt{\left(\frac{h^2FD^* \; h^2MS}{h^2MD^* \; h^2FS}\right)}$$

where h^2 represents narrow sense heritability estimates for all possible parent-offspring combinations: father-daughter (FD), mother-son (MS), mother-daughter (MD), and father-son (FS) (Lynch and Walsh 1998). Narrow sense heritability is the proportion of variance in a trait that is due to additive genetic factors, calculated as the ratio of additive genetic variance to total phenotypic variance (Lynch and Walsh 1998). Additive genetic variance is an important parameter in quantitative genetic research, because it implies the trait's evolvability (Falconer and Mackay 1996; Lynch and Walsh 1998). Empirical studies that test the correlation between r_{MF} and SD yield mixed results, though generally confirm the expected negative correlation (Poissant et al. 2010).

Body size is among the physical attributes of organisms that influence most other aspects of their biology (Roff 1992), as it correlates closely with life-history traits in vertebrates and invertebrates (Peters 1983; Honěk 1993). Body size notably affects individuals' performance in foraging, as well as juvenile development time and longevity (Kessler 1971; Simpson 1995). In females, body size influences fecundity, larger females producing more offspring (Kessler 1971; Fritz and Morse 1985; Gonzaga and Vasconcellos-Neto 2001; Branson 2008). On the other hand, male body size influences performance in direct and indirect male-male competition (Rosenberg and Enquist 1991). Due to sex-specific selection pressures, the optimal body size may differ for males and females, resulting in sexual size dimorphism (SSD; Blanckenhorn 2005).

Spiders are known for female-biased SSD, in some cases so extreme that females weigh 125 times more than males (Kuntner et al. 2012; Cheng and Kuntner 2014). While studies agree that female body size in spiders strongly responds to fecundity selection (Head 1995; Reeve and Fairbairn 1996), it is less clear what selection pressures act on males (Kuntner and Elgar 2014). For example, scramble competition, gravity, sexual cannibalism, and mortality are all believed to select for small male size, while male-male competition favors large males (Elgar 1991; Moya-Laraño et al. 2002; Maklakov et al. 2004; Blanckenhorn 2005; Foellmer and Fairbairn 2005; Kasumovic et al. 2006; Kasumovic and Andrade 2009; Danielson-François et al. 2012; Kuntner and Elgar 2014). These diverse, sex-specific selection pressures along with a large range of spider SSD make spiders suitable organisms for the study of the relationship between size heritability and SSD.

Here, we explore body mass heritability in three species of orb-web spiders exhibiting varying degrees of female-biased SSD: bridge spider (*Larinioides sclopetarius*), walnut orb-weaver (*Nuctenea umbratica*), and silver-sided sector spider (*Zygiella x-notata*). Using a fixed size parameter, such as carapace width, provides the optimal size proxy for quantitative genetic studies, as it is largely independent of individual body condition and does not change after maturation. However, as we explain in the methods, we use body mass as a proxy for body size, because these two parameters strongly correlate in invertebrates, including spiders (Honěk 1993; Legaspi and Legaspi 2005; Branson 2008; Neumann and Schneider 2015).

Data on body mass, combined with a record of the individuals' pedigrees, enable the estimation of body mass heritability and calculation of r_{MF}. We predict r_{MF} to be higher in more size monomorphic and lower in more size dimorphic species. When body size is a strongly sexually dimorphic trait, the degree of same-sex size heritability is expected to be high and the degree of opposite-sex size heritability low. On the other hand, more size monomorphic species are expected to exhibit similar degrees of heritability from both parents. In other words, we predict to detect relatively higher h^2_{MD} and h^2_{FS} and lower h^2_{FD} and h^2_{MS} when SSD is high.

Material and methods

Studied species

We chose three species of spiders that are easily accessible and collectable in the field in Slovenia. They all belong to the same family: the classical orb-web spiders (Araneidae). While we acknowledge that *Larinioides* and *Nuctenea* are much more closely related than either is to *Zygiella* (Gregorič et al. 2015), this study aims at comparing araneids with similar life histories and varying degrees of SSD.

The bridge spider, *Larinioides sclopetarius* (Clerck 1757), is a common Holarctic species. High density populations consisting of individuals of both sexes and different ages colonize urban constructions near bodies of water (Heiling and Herberstein 1998). Bridge spiders exhibit a pronounced, female-biased SSD. Females have a longer developmental time than males—under a high feeding regime, males mature, on average, 26 days earlier than do females (Kleinteich and Schneider 2010). While females build, maintain, and defend their webs, males live kleptoparasitically on the females' webs (Heiling and Herberstein 1998). Prior laboratory studies found that *L. sclopetarius* exhibit high developmental plasticity depending on food availability, a short life cycle of about 60 days at ample food, and high reproductive output of up to 12 viable egg cases (Kleinteich and Schneider 2011; own data).

The silver-sided sector spider, *Zygiella x-notata* (Clerck 1757), is also a common Holarctic species that often inhabits human constructions such as walls, fences, and window frames but can also inhabit urban or pristine vegetation (Leborgne and Pasquet 1987). *Zygiella x-notata* females are moderately larger than their male conspecifics and need

approximately 14 days longer time to reach maturity (Mayntz et al. 2003). They exhibit developmental plasticity depended on food availability, have an intermediate developmental time of 160 days at ample food (Mayntz et al. 2003), and a reproductive output of up to eight viable egg cases (own data).

The walnut orb-weaver, *Nuctenea umbratica* (Clerck 1757), is a common central European species. It prefers landscapes with semi-open habitats, such as forest edge, hedgerows, orchards, and single trees (Horváth and Szinetár 2002; Horváth et al. 2005; Bucher et al. 2010). Females are larger than males and develop more slowly (Kralj-Fišer et al. 2014). Its female-biased SSD is intermediate among the three studied species. If well fed, males mature on average 30 days earlier than females (Kralj-Fišer et al. 2014). In comparison to the previous two species, *N. umbratica* development is more canalized, meaning that spiders' phenotype is similar regardless of food availability. In comparison to other two species, the walnut orb-weaver exhibits a long life cycle (240 days at ample food) and a low reproductive output of up to four viable egg cases (Kralj-Fišer et al. 2014; own data).

Field collection

Subadult males and females were collected in the field and transferred to the laboratory to be reared to maturity. *Larinioides sclopetarius* were collected from buildings, fences, and bridges along riverbanks in Hamburg, Germany (53.577401, 10.009699), in September 2010. *Zygiella x-notata* were collected from man-made constructions along the Vipava riverbank, Slovenia (45.844605, 13.963604), in May 2012. *Nuctenea umbratica* were collected from their webs on trees and hedgerows along the Ljubljanica riverbank, Slovenia (46.045093, 14.506048), between May and July 2011.

Laboratory rearing and data collection

Field-collected spiders were reared under standardized laboratory conditions (room temperature, L/D = 10:14). They were kept in 200-ml plastic cups and fed ad libitum with fruit flies (*Drosophila* sp.) until the final molt. Upon maturation, females were relocated into plastic frames ($36 \times 36 \times 6$ cm) and fed two blow flies (*Calliphora* sp.) twice a week. Because adult males cease to construct webs, they were left in the original plastic cups, subjected to the same feeding treatment as females. Throughout the study, the spiders were water-sprayed 5 days a week to maintain humidity. At maturity and while still virgin, all spiders were weighed (accuracy of 0.01 mg). We measured 59 *L. sclopetarius* spiders (N females = 29, N males = 30; age at weighing = 8.5 ± 7.25 days), 53 *Z. x-notata* spiders (N females = 29, N males = 24; age at weighing = 28.28 ± 16.09 days), and 95 *N. umbratica* spiders

(N females = 41, N males = 54; age at weighing = 1.04 ± 0.41 days).

All spiders were then used for studies of assortative mating (Kralj-Fišer and Schneider 2012; Kralj-Fišer et al. 2017). Males and females were mated according to their aggressiveness score; however, aggressiveness did not show any correlation with body mass (Kralj-Fišer and Schneider 2012), meaning that spiders were mated randomly in respect to body mass. We initiated mating encounters that lasted 24 h (to allow time for successful mating) by placing a male on a female's web with a paintbrush. We then separated the couples and continued rearing the spiders individually until their natural death. We monitored the frames for deposited egg cases, which we collected and stored at room temperature until hatching. After the second molt, we placed a subset of spiderlings from each parental pair into individual 200 ml plastic cups to be reared under standardized conditions. Upon molting to adulthood and while still virgin, we weighed the spiders like those of the parental generation. In *L. sclopetarius*, we weighed five male and five female offspring per family, i.e., parental pair (N families = 29). In strongly sex-biased clutches, the data thus include fewer than ten spiders. In *Z. x-notata* (N families = 29) and *N. umbratica* (N families = 41), we weighed three males and three females per family. In the offspring generation, we measured a total of 269 *L. sclopetarius* spiders (N females = 134, N males = 125; age at weighing = 6.35 ± 6.56 days), 132 *Z. x-notata* spiders (N females = 63, N males = 69; age at weighing = 16.59 ± 7.80 days), and 90 *N. umbratica* spiders (N females = 46, N males = 44; age at weighing = 47.33 ± 20.83 days).

Spiders from the offspring generation were used for further experiments (Kralj-Fišer and Schneider 2012), during which many were cannibalized. The rest were not preserved in ethanol, because identification markings made on the spiders wore off during the experiments, and individual recognition of the surviving spiders was no longer possible. Fixed size data could not be reliably obtained, so we used body mass as a proxy for body size. Female spiders of all three species showed significant weight gain with age (own data). We accounted for this using ordinary least squares regression in SDI calculations and by including age as a covariate in MCMCglmm analyses.

Statistical analyses

We used the size dimorphism index (SDI; Lovich and Gibbons 1992) to quantify SSD, pooling data for both generations for each species:

$$\text{SDI} = \frac{females' \ mean \ mass}{males' \ mean \ mass} - 1$$

This SDI includes the subtraction of 1 if females are the larger sex, in order to achieve directionality of the index. Consequently, the resulting index only reflects the true proportion of SSD after the addition of 1 (Lovich and Gibbons 1992).

We calculated estimates of body mass heritability following Wilson et al. (2010) and de Villemereuil (2012), performing Markov Chain Monte Carlo linear mixed model (MCMCglmm) analyses in R (version 2.15.3, R Core Team 2013; Hadfield 2010). We ran the protocol using two priors, differing in the assumed ratio between residual and genetic variance in body mass. The first assumes all variance is either residual or genetic, and the second assumes half of the total variance to each component (shown in Appendices S1 and S2, respectively). Using the first prior resulted in a greater effective sample size and was thus used for further analyses.

In order to define relatedness between individuals, a pedigree was constructed, containing each individual included in the analysis. Individuals of the parental generation were field-collected and their family tree is unknown, so their parents were marked with N/A. Heritability estimates were then calculated for every parent-offspring combination for each species, with sex and age at weighing as covariates and pedigree as a random factor. Appendix S1 lists the full R script used in the analyses. Cross-sex genetic correlation (r_{MF}) was assessed for each species after Lynch and Walsh (1998).

The model we used is relatively general, because sample sizes proved much too small to work with more complex models. We ran a complex model that accounted for sibling covariation; however, the resulting credible intervals were extremely wide suggesting very high uncertainty. Accurate r_{MF} estimations using such a model would require sample sizes of thousands of individuals from hundreds of families (Hadfield, personal communication).

Results

In all three species, females were heavier than males (for average body mass with standard deviation for each species, see Table 1; for error bars of average body mass with confidence intervals by sex, generation, and species, see Fig. 1). *Larinioides sclopetarius* was the most size dimorphic (SDI = 0.847), *Z. x-notata* the least (SDI = 0.462), and *N. umbratica* was moderately size dimorphic (SDI = 0.597). This is also visible from Fig. 1, where the difference between female and male mean body mass is the biggest in *L. sclopetarius* and the smallest in *Z. x-notata*.

We found moderate heritability of body mass in all three species (*L. sclopetarius*, $h^2 = 0.208$; *N. umbratica*, $h^2 = 0.210$; *Z. x-notata*, $h^2 = 0.390$; Table 2) when pooling all data. Maternal heritability estimates were 0.311 in *L. sclopetarius*, 0.234 in *N. umbratica*, and 0.538 in *Z. x-notata* (Table 2).

Paternal heritability estimates were 0.402, 0.283, and 0.481 in *L. sclopetarius*, *N. umbratica*, and *Z. x-notata*, respectively (Table 2).

Against our prediction, in the most size dimorphic species *L. sclopetarius*, mean heritability estimates for same-sex combinations ($h^2_{MD} = 0.300$, $h^2_{FS} = 0.350$) were lower than mean heritability estimates for opposite-sex combinations ($h^2_{MS} = 0.484$, $h^2_{FD} = 0.410$; Table 2). In *N. umbratica*, daughters have higher mean heritability estimates than sons through both parents; mean h^2_{MD} was higher than mean h^2_{MS}, while mean h^2_{FD} was higher than mean h^2_{FS} ($h^2_{MD} = 0.453$, $h^2_{FS} = 0.291$, $h^2_{MS} = 0.241$, $h^2_{FD} = 0.465$; Table 2). Mean heritability estimates in *Z. x-notata* were similar and high when estimated through fathers and mothers with somewhat higher mean heritability estimates to daughters than sons ($h^2_{MD} = 0.472$, $h^2_{FS} = 0.587$, $h^2_{MS} = 0.572$, $h^2_{FD} = 0.517$; Table 2). It should be noted that in all three species, credible intervals for all four heritability combinations largely overlap (Table 2).

In contrast to our prediction that cross-sex genetic correlation would be lower in more size-dimorphic species, r_{MF} estimates in the tested species were all close to 1: *L. sclopetarius* ($r_{MF} = 1.375$), *N. umbratica* ($r_{MF} = 0.922$), and *Z. x-notata* ($r_{MF} = 1.033$).

Discussion

The evolution of sexual dimorphism is frequently explained by low cross-sex genetic correlation ($r_{MF} << 1$), which would allow both sexes to evolve their respective optimal phenotypes (Lande 1980). Considering body size or mass, low cross-sex genetic correlation should be more typical of sexually size dimorphic rather than monomorphic species. We tested this hypothesis in three orb-web spider species with body mass sexual dimorphism indices (SDI) of 0.85 (*L. sclopetarius*), 0.60 (*N. umbratica*), and 0.46 (*Z. x-notata*), predicting that cross-sex genetic correlation would be lowest in *L. sclopetarius* and highest in *Z. x-notata*. Contrary to this prediction, we found comparably high cross-sex genetic correlation in all three species. Our results refute a clear relationship between the level of SDI and r_{MF}.

We detect no sex-specific heritability pattern of body mass in any species. When looking at general, cross-population body mass heritability from pooled data, *L. sclopetarius* (0.21) and *N. umbratica* (0.22) exhibit a moderate influence of additive genetic factors on body mass, while this influence is somewhat higher in *Z. x-notata* (0.39). In comparison, mass heritability is estimated between 0.37 and 0.65 in the seed beetle *Callosobruchus maculatus* (Fabricius 1775) (Fox et al. 2004a), 0.48 in the moth *Utetheisa ornatrix* (Linnaeus 1758) (Iyengar and Eisner 1999), and 0.6 in the cellar spider *Pholcus phalangioides* (Füssli 1775) (Uhl et al. 2004). Our detected heritability values are lower compared to those

Table 1 Average body mass ±
95% standard deviation by sex
and sexual dimorphism indices
calculated from pooled data for
each species

	Female body mass average (grams)	Male body mass average (grams)	Sexual dimorphism index (SDI)
L. sclopetarius	0.109 ± 0.043	0.059 ± 0.012	0.847
N. umbratica	0.107 ± 0.030	0.067 ± 0.021	0.597
Z. x-notata	0.038 ± 0.012	0.026 ± 0.006	0.462

above. It may be worth noting that the species we studied show higher female-biased SSD.

In theory, sex-specific selection should lead to greater heritability between same-sex individuals than opposite-sex individuals (Bonduriansky and Rowe 2005a). Female offspring should be more likely to inherit alleles that benefit female fitness from their mothers than from their fathers, which are not subjected to sexual selection for that trait (Bonduriansky and Rowe 2005a). Our results, however, do not adhere to this predicted pattern. A possible proximate explanation for the observed deviation from the hypothetical pattern of heritability is the existence of parent-of-origin influence on gene expression, also known as genomic imprinting (Day and Bonduriansky 2004; Bonduriansky and Chenoweth 2009). Our study did not test for effects of genomic imprinting, so further analyses would be needed to confirm its influence.

Importantly, existing studies of heritability in animals are largely restricted to laboratory-kept populations. Arguably, heritability estimates in laboratory populations under controlled conditions tend to be greater than in natural populations (Riska et al. 1989). However, a major problem with the study of wild populations is the construction of a pedigree, essential in heritability studies (Lynch and Walsh 1998). Our study constructs the offspring (though not the parental) pedigree and standardizes the environmental factors influencing the offspring, which may be reflected in narrower 95% confidence intervals in the offspring generation compared to the parental (Fig. 1). In summation, our body mass heritability estimates could be lower due to such methodological differences in comparison to studies on solely laboratory-kept populations.

We fail to support our prediction that cross-genetic correlations for body mass will be significantly lower than 1 in all three species, with r_{MF} being the highest in the species with the lowest SDI and vice-versa. Contrary to our expectations, all three r_{MF} estimates in the tested species were close to 1. Our estimated values for r_{MF} resemble those for size monomorphic arthropods (cellar spider *P. phalangioides*, SDI = 0.07, r_{MF} = 0.94, Uhl et al. 2004; black tiger prawn *Penaeus monodon* (Fabricius 1798), SDI = 0.09, r_{MF} = 0.97, Kenway et al. 2006; black field cricket *Teleogryllus commodus* (Walker 1869), SDI not listed, r_{MF} = 0.96, Zajitschek et al. 2007).
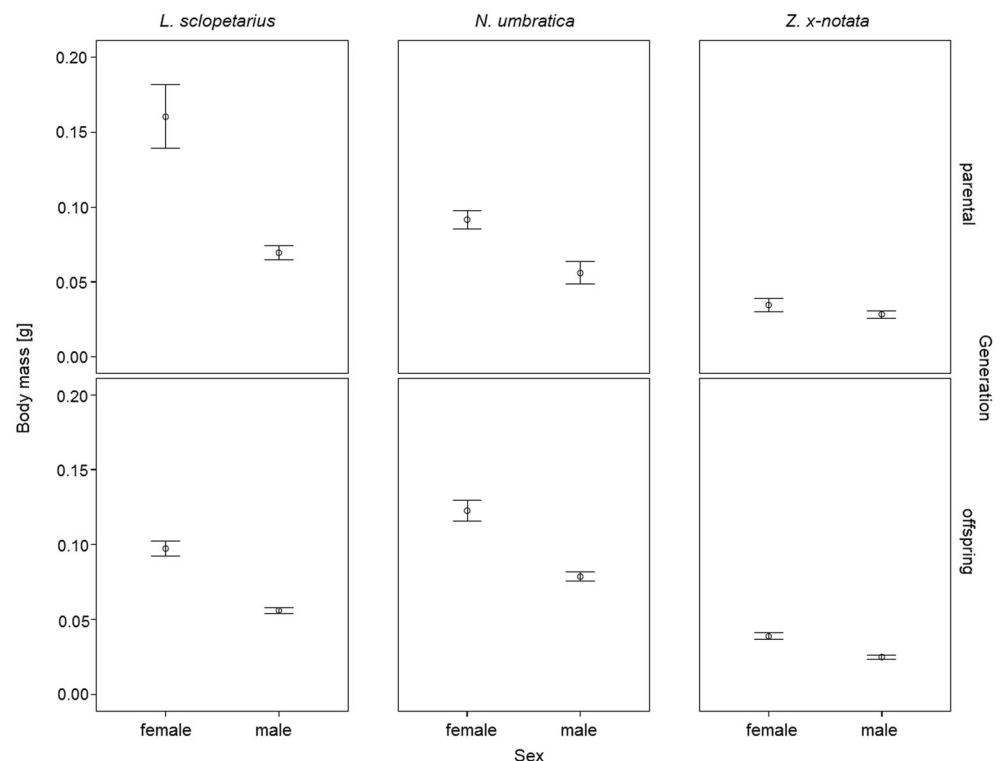
Fig. 1 Mean body mass of males and females in parental (upper panels) and offspring (lower panels) generations of the three study species. Whiskers are 95% confidence intervals

Table 2 Heritability estimates and 95% credible intervals (Cred. int.) for every parent-offspring combination in each species

	Mothers	Cred. int.	Fathers	Cred. int.	All parents	Cred. int.
Larinioides sclopetarius ($N = 318$)						
Daughters	0.300	0.110–0.530	0.410	0.166–0.670	0.227	0.091–0.379
Sons	0.484	0.281–0.710	0.350	0.123–0.584	0.411	0.246–0.581
All offspring	0.311	0.130–0.521	0.402	0.204–0.610	0.208	0.107–0.311
Nuctenea umbratica ($N = 181$)						
Daughters	0.453	0.220–0.722	0.465	0.260–0.686	0.369	0.182–0.563
Sons	0.241	0.078–0.444	0.291	0.074–0.521	0.196	0.074–0.347
All offspring	0.234	0.091–0.407	0.283	0.097–0.505	0.210	0.084–0.348
Zygiella x-notata ($N = 185$)						
Daughters	0.472	0.149–0.815	0.517	0.244–0.798	0.387	0.152–0.640
Sons	0.572	0.282–0.844	0.587	0.280–0.895	0.497	0.236–0.746
All offspring	0.538	0.264–0.807	0.481	0.248–0.722	0.390	0.181–0.600

For a relevant comparison, one needs to parallel our study to those on invertebrate species with SDI scores over 0.4. To list some examples, eye span to body length ratio in the stalk-eyed fly (*Cyrtodiopsis dalmanni* (Wiedemann 1830), SD = 0.41) shows a cross-genetic correlation of 0.29 (Wilkinson 1993), while antenna length in the waltzing fly (*Prochyliza xanthostoma* (Walker 1849), SD = 0.62) shows a cross-genetic correlation of 0.21 (Bonduriansky and Rowe 2005b). In water striders (*Aquarius remiges* (Say 1832), SDI = 0.7), however, r_{MF} estimates range from 0.17 (mid-femur length) to 1.01 (abdomen length) (Preziosi and Roff 1998). In general, a negative relationship between SDI and r_{MF} does exist (Poissant et al. 2010), but there are several examples that do not conform to the rule.

A wide range of cross-sex genetic correlation scores has been found across several studies of sexual size dimorphism, both in and among populations. For instance, the cross-sex genetic correlation for body mass differed substantially between two populations of the seed beetle *C. maculatus* (south India: r_{MF} = 0.28, Burkina Faso: r_{MF} = 0.91, Fox et al. 2004a). In other words, the two populations differed in the genetic basis for sexual dimorphism. The reasons behind this are not fully understood, but several possible contributing factors have been proposed. Fox et al. (2004b) stress the importance of non-additive genetic factors (gene interactions), such as dominance and epistasis, and the maternal effect. Additionally, heritability estimates may be influenced by the so-called common environment effect, which attributes similarity between organisms to the common environment in which they live, rather than their genetic makeup (Roff 1997; Uhl et al. 2004). The actual influence of non-additive genetic factors and maternal effect on offspring fitness remains unclear and was not controlled for in the present study, while the effect of a common environment was minimized by keeping each spider in its own container.

To recap the theory, when selection acts in sex-specific directions, the evolution of sexual dimorphism should be facilitated by low r_{MF} values (Lande 1980). However, several scenarios may account for a pronounced SSD in the absence of clear sex-specific genotypes. First, model simulations by Reeve and Fairbairn (2001) allow for evolution of sexual dimorphism even while maintaining relatively high r_{MF}, if only allele frequencies change, rather than the genetic architecture as a whole. This suggests that high r_{MF} can point to either sexual monomorphism or sexual dimorphism with a resolved intralocus sexual conflict (Bonduriansky and Chenoweth 2009). Therefore, it may be that in our tested species, intralocus sexual conflict is resolved through allele frequency shifts rather than changes in genetic makeup. Alternatively, sex-specific gene expression may underlie high SSD despite a genetic base shared between males and females. These scenarios require quantitative genetic or transcriptomic tests in species with varying degrees of SSD.

The unexpectedly high r_{MF} scores likewise require a methodological clarification. The r_{MF} equation (Lynch and Walsh 1998) assumes heritability to be higher in same-sex (mother-daughter, father-son) than opposite-sex pairings (mother-son, father-daughter). If that is true, the resulting correlation value must fall within the mathematically logical range of values between 0 and 1. However, the biological reality based on our results is that opposite-sex pairings may have higher heritability values than same-sex pairings. Consequently, the numerator is greater than the denominator and the resulting value exceeds 1 (also see Reeve and Fairbairn 2001). Thus, values above 1 may be valid and are indeed common in r_{MF} studies (Preziosi and Roff 1998; Fox et al. 2004a; Bonduriansky and Rowe 2005a).

We need to acknowledge the drawbacks of this study. Its foremost weakness is the use of body mass as a proxy for body size, for reasons explained in the methods. Additionally, sample sizes could be increased, allowing for more complex

statistical analyses. As suggested by Hadfield (personal communication), we would need thousands of individuals for reliable r_{MF} analyses using complex MCMCglmm protocols. However, quantitative genetic studies on a wide range of diverse species are needed for a general understanding of trait heritability and the evolution of SSD in spiders and we trust this study is a valuable contribution towards that aim.

In conclusion, our findings do not support the hypothesis that SSD is negatively correlated with cross-sex genetic correlation if assessed via same-sex and opposite-sex heritability estimates. It seems that a sex-specific genetic architecture is not necessary for the evolution of a sexually dimorphic trait.

References

Blanckenhorn WU (2005) Behavioral causes and consequences of sexual size dimorphism. Ethology 111(11):977–1016. https://doi.org/10.1111/j.1439-0310.2005.01147.x

Bonduriansky R, Chenoweth SF (2009) Intralocus sexual conflict. Trends Ecol Evol 24(5):280–288. https://doi.org/10.1016/j.tree.2008.12.005

Bonduriansky R, Rowe L (2005a) Intralocus sexual conflict and the genetic architecture of sexually dimorphic traits in *Prochyliza xanthostoma* (Diptera: Piophilidae). Evolution 59(9):1965–1975. https://doi.org/10.1554/05-236.1

Bonduriansky R, Rowe L (2005b) Sexual selection, genetic architecture, and the condition dependence of body shape in the sexually dimorphic fly *Prochyliza xanthostoma* (Piophilidae). Evolution 59(1):138–151. https://doi.org/10.1554/04-445

Branson DH (2008) Influence of individual body size on reproductive traits in melanopline grasshoppers (Orthoptera: Acrididae). J Orthop Res 17(2):259–263. https://doi.org/10.1665/1082-6467-17.2.259

Bucher R, Herrmann JD, Schüepp C, Herzog F, Schmidt M (2010) Arthropod colonisation of trees in fragmented landscapes depends on species traits. Open Ecol J 3(1):111–117. https://doi.org/10.2174/1874213001003010111

Cheng RC, Kuntner M (2014) Phylogeny suggests nondirectional and isometric evolution of sexual size dimorphism in argiopine spiders. Evolution 68(10):2861–2872. https://doi.org/10.1111/evo.12504

Danielson-François A, Hou C, Cole N, Tso IM (2012) Scramble competition for moulting females as a driving force for extreme male dwarfism in spiders. Anim Behav 84(4):937–945. https://doi.org/10.1016/j.anbehav.2012.07.018

Day T, Bonduriansky R (2004) Intralocus sexual conflict can drive the evolution of genomic imprinting. Genetics 167(4):1537–1546. https://doi.org/10.1534/genetics.103.026211

de Villemereuil P (2012) Estimation of a biological trait heritability using the animal model. How to use the MCMCglmm R package. Retrieved from http://devillemereuil.legtux.org/wp-content/uploads/2012/12/tuto_en.pdf. Accessed 6 October 2016

Elgar MA (1991) Sexual cannibalism, size dimorphism, and courtship behavior in orb-weaving spiders (Araneidae). Evolution 45(2):444–448. https://doi.org/10.1111/j.1558-5646.1991.tb04419.x

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th edn. Longman, Essex

Foellmer MW, Fairbairn DJ (2005) Competing dwarf males: sexual selection in an orb-weaving spider. J Evol Biol 18(3):629–641. https://doi.org/10.1111/j.1420-9101.2005.00868.x

Fox CW, Bush ML, Roff DA, Wallin WG (2004a) Evolutionary genetics of lifespan and mortality rates in two populations of the seed beetle, *Callosobruchus maculatus*. Heredity 92(3):170–181. https://doi.org/10.1038/sj.hdy.6800383

Fox CW, Czesak ME, Wallin WG (2004b) Complex genetic architecture of population differences in adult lifespan of a beetle: nonadditive inheritance, gender differences, body size and a large maternal effect. J Evol Biol 17(5):1007–1017. https://doi.org/10.1111/j.1420-9101.2004.00752.x

Fritz RS, Morse DH (1985) Reproductive success and foraging of the crab spider *Misumena vatia*. Oecologia 65(2):194–200. https://doi.org/10.1007/BF00379217

Gonzaga MDO, Vasconcellos-Neto J (2001) Female body size, fecundity parameters and foundation of new colonies in *Anelosimus jabaquara* (Araneae, Theridiidae). Insect Soc 48(2):94–100. https://doi.org/10.1007/PL00001765

Gregorič M, Agnarsson I, Blackledge TA, Kuntner M (2015) Phylogenetic position and composition of Zygiellinae and *Caerostris*, with new insight into orb-web evolution and gigantism. Zool J Linnean Soc 175(2):225–243. https://doi.org/10.1111/zoj.12281

Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J Stat Softw 33:1–22

Head G (1995) Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Araneae). Evolution 49(4):776–781. https://doi.org/10.1111/j.1558-5646.1995.tb02313.x

Heiling AM, Herberstein ME (1998) Activity patterns in different developmental stages and sexes of *Larinioides sclopetarius* (Clerck) (Araneae, Araneidae). In: Selden PA (ed) Proceedings of the 17th European Colloquium of Arachnology. British Arachnological Society, Edinburgh, pp 211–214

Honěk A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66(3):483–492. https://doi.org/10.2307/3544943

Horváth R, Szinetár C (2002) Ecofaunistical study of bark-dwelling spiders (Araneae) on black pine (*Pinus nigra*) in urban and forest habitats. Acta Biol Debrecina 24:87–101

Horváth R, Lengyel S, Szinetár C, Jakab L (2005) The effect of prey availability on spider assemblages on European black pine (*Pinus nigra*) bark: spatial patterns and guild structure. Can J Zool 83(2):324–335. https://doi.org/10.1139/z05-009

Iyengar VK, Eisner T (1999) Heritability of body mass, a sexually selected trait, in an arctiid moth (*Utetheisa ornatrix*). Proc Natl Acad Sci 96(16):9169–9171. https://doi.org/10.1073/pnas.96.16.9169

Kasumovic MM, Andrade MC (2009) A change in competitive context reverses sexual selection on male size. J Evol Biol 22(2):324–333. https://doi.org/10.1111/j.1420-9101.2008.01648.x

Kasumovic MM, Bruce MJ, Herberstein ME, Andrade MC (2006) Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). Behav Ecol 18(1):189–195. https://doi.org/10.1093/beheco/arl072

Kenway M, Macbeth M, Salmon M, McPhee C, Benzie J, Wilson K, Knibb W (2006) Heritability and genetic correlations of growth and survival in black tiger prawn *Penaeus monodon* reared in tanks. Aquaculture 259(1-4):138–145. https://doi.org/10.1016/j.aquaculture.2006.05.042

Kessler A (1971) Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia 8(1):93–109. https://doi.org/10.1007/BF00345629

Kleinteich A, Schneider JM (2010) Evidence for Rensch's rule in an orb-web spider with moderate sexual size dimorphism. Evol Ecol Res 12:667–683

Kleinteich A, Schneider JM (2011) Developmental strategies in an invasive spider: constraints and plasticity. Ecol Entomol 36(1):82–93. https://doi.org/10.1111/j.1365-2311.2010.01249.x

Kralj-Fišer S, Schneider JM (2012) Individual behavioural consistency and plasticity in an urban spider. Anim Behav 84(1):197–204. https://doi.org/10.1016/j.anbehav.2012.04.032

Kralj-Fišer S, Čelik T, Lokovšek T, Šuen K, Šiling R, Kuntner M (2014) Development and growth in synanthropic species: plasticity and constraints. Naturwissenschaften 101(7):565–575. https://doi.org/10.1007/s00114-014-1194-y

Kralj-Fišer S, Hebets EA, Kuntner M (2017) Different patterns of behavioral variation across and within species of spiders with differing degrees of urbanization. Behav Ecol Sociobiol 71(8):125. https://doi.org/10.1007/s00265-017-2353-x

Kuntner M, Elgar MA (2014) Evolution and maintenance of sexual size dimorphism: aligning phylogenetic and experimental evidence. Front Ecol Evol 2:26. https://doi.org/10.3389/fevo.2014.00026

Kuntner M, Zhang S, Gregorič M, Li D (2012) *Nephila* female gigantism attained through post-maturity molting. J Arachnol 40(3):345–347. https://doi.org/10.1636/B12-03.1

Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34(2):292–305. https://doi.org/10.1111/j.1558-5646.1980.tb04817.x

Leborgne R, Pasquet A (1987) Influences of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck). Behav Ecol Sociobiol 20(3):203–208. https://doi.org/10.1007/BF00299734

Legaspi JC, Legaspi BC Jr (2005) Body weights and egg loads in field-collected *Podisus maculiventris* (Heteroptera: Pentatomidae). Fla Entomol 88(1):38–42. https://doi.org/10.1653/0015-4040(2005)088[0038:BWAELI]2.0.CO;2

Lovich JE, Gibbons JW (1992) A review of techniques for quantifying sexual size dimorphism. Growth Dev Aging 56(4):269–281

Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer, Sunderland

Maklakov AA, Bilde T, Lubin Y (2004) Sexual selection for increased male body size and protandry in a spider. Anim Behav 68(5):1041–1048. https://doi.org/10.1016/j.anbehav.2004.02.010

Mayntz D, Toft S, Vollrath F (2003) Effects of prey quality and availability on the life history of a trap-building predator. Oikos 101(3):631–638. https://doi.org/10.1034/j.1600-0706.2003.12408.x

Moya-Laraño J, Halaj J, Wise DH (2002) Climbing to reach females: Romeo should be small. Evolution 56(2):420–425. https://doi.org/10.1554/0014-3820(2002)056[0420:CTRFRS]2.0.CO;2

Neumann R, Schneider JM (2015) Differential investment and size-related mating strategies facilitate extreme size variation in contesting male spiders. Anim Behav 101:107–115. https://doi.org/10.1016/j.anbehav.2014.12.027

Pennell TM, Morrow EH (2013) Two sexes, one genome: the evolutionary dynamics of intralocus sexual conflict. Ecol Evol 3(6):1819–1834. https://doi.org/10.1002/ece3.540

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511608551

Poissant J, Wilson AJ, Coltman DW (2010) Sex-specific genetic variance and the evolution of sexual dimorphism: a systematic review of cross-sex genetic correlations. Evolution 64(1):97–107. https://doi.org/10.1111/j.1558-5646.2009.00793.x

Preziosi RF, Roff DA (1998) Evidence of genetic isolation between sexually monomorphic and sexually dimorphic traits in the water strider *Aquarius remigis*. Heredity 81(1):92–99. https://doi.org/10.1046/j.1365-2540.1998.00380.x

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org/

Reeve JP, Fairbairn DJ (1996) Sexual size dimorphism as a correlated response to selection on body size: an empirical test of the quantitative genetic model. Evolution 50(5):1927–1938. https://doi.org/10.1111/j.1558-5646.1996.tb03580.x

Reeve JP, Fairbairn DJ (2001) Predicting the evolution of sexual size dimorphism. J Evol Biol 14(2):244–254. https://doi.org/10.1046/j.1420-9101.2001.00276.x

Riska B, Prout T, Turelli M (1989) Laboratory estimates of heritabilities and genetic correlations in nature. Genetics 123(4):865–871

Roff DA (1992) Age and size at maturity. In: Roff DA (ed) The evolution of life histories: theory and analysis. Chapman & Hall, New York, pp 179–241

Roff DA (1997) The genetic correlation. In: Roff DA (ed) Evolutionary quantitative genetics. Chapman & Hall, London, pp 73–117. https://doi.org/10.1007/978-1-4615-4080-9_3

Rosenberg RH, Enquist M (1991) Contest behaviour in Weidemeyer's admiral butterfly *Limenitis weidemeyerii* (Nymphalidae): the effect of size and residency. Anim Behav 42(5):805–811. https://doi.org/10.1016/S0003-3472(05)80124-1

Simpson MR (1995) Covariation of spider egg and clutch size: the influence of foraging and parental care. Ecology 76(3):795–800. https://doi.org/10.2307/1939345

Uhl G, Schmitt S, Schäfer MA, Blanckenhorn W (2004) Food and sex-specific growth strategies in a spider. Evol Ecol Res 6:523–540

Wilkinson GS (1993) Artificial sexual selection alters allometry in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). Genet Res 62(03):213–222. https://doi.org/10.1017/S001667230003192X

Wilson AJ, Reale D, Clements MN, Morrissey MM, Postma E, Walling CA, Kruuk LE, Nussey DH (2010) An ecologist's guide to the animal model. J Anim Ecol 79(1):13–26. https://doi.org/10.1111/j.1365-2656.2009.01639.x

Zajitschek F, Hunt J, Zajitschek SR, Jennions MD, Brooks R (2007) No intra-locus sexual conflict over reproductive fitness or ageing in field crickets. PLoS One 2(1):e155. https://doi.org/10.1371/journal.pone.0000155