Sexual dimorphism in the badlands cricket (Orthoptera, Gryllinae, *Gryllus personatus*)

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Abstract

Sexual dimorphism (SD) is a common phenomenon in sexual species and can manifest in a variety of ways. Sexual size dimorphism (SSD) is commonly investigated, but it can be confounded with sexual shape dimorphism (SShD) if multivariate measures of size are not used. Univariate studies may also overestimate the prevalence or direction of SSD when the sexes are strikingly different in shape, which may be an issue in taxa such as Orthoptera and other terrestrial arthropods where maximum body size is strongly constrained. Here we tested for the occurrence of both SSD and SShD in the badlands cricket *Gryllus personatus* (Orthoptera, Gryllinae). We measured four body size dimensions—maxillae span, head width, pronotum length, and mean hind femur length—and used multivariate methods to test whether male and female adult badlands crickets were sexually dimorphic in size and/or shape. All the univariate dimensions were sexually dimorphic, with males having wider heads and maxillae than females and females having longer pronota and hind femora than males, which indicates SShD. However, multivariate methods failed to detect SSD, instead confirming that the sexes primarily differ in body shape. We show how a simple ratio of head width to pronotum length captures SShD in badlands crickets and apply it to iNaturalist, a citizen science platform, to broaden our findings. We propose that orthopterists studying SD minimally measure head width, pronotum length, and hind femur length as a standard that will allow a more repeatable and generalizable assessment of the prevalence and direction of both SSD and SShD.

Keywords

body size, geometric mean size, Gryllinae, sexual shape dimorphism, sexual size dimorphism

Introduction

Intraspecific differences between males and females, or sexual dimorphism (SD), are common in sexually reproducing organisms (Darwin 1871, Andersson 1994, Fairbairn et al. 2007, Stillwell et al. 2010) and are thought to be caused by either intersexual competition for resources (Selander 1966), sex-specific equilibria (Blanckenhorn 2005), or some combination thereof. SD can take a variety of forms,

from differences in behavior (e.g., parental care, reviewed in Kokko and Jennions 2008), development (e.g., Esperk et al. 2007, reviewed in Hopkins and Kopp 2021), and immunity (e.g., Bagchi et al. 2021, reviewed in Kelly et al. 2018) to differences in overall body size (sexual size dimorphism, SSD; reviewed in Fairbairn et al. 2007) and body shape (sexual shape dimorphism [SShD], e.g., Table 1). These latter two are of special interest because they: 1) are relatively easy to measure, 2) can impact other dimorphisms (e.g., sex differences in mobility, reviewed in Herberstein et al. 2017) as well as important life history traits (e.g., fecundity, reviewed for spiders in Foellmer and Moya-Laraño 2007), and 3) unlike other dimorphisms, SSD and SShD are preserved in the fossil record making it possible to study their long-term evolution (e.g., Martins et al. 2020). In organisms such as arthropods that have an exoskeleton, maximum body size and therefore SSD may be evolutionarily constrained (reviewed in Whitman 2008 and references therein), placing greater selection pressure on the evolution of body shape and thus SShD.

The order Orthoptera (crickets, katydids, grasshoppers, and allies) display one of the highest degrees of SSD among insects (Stillwell et al. 2010), with most species displaying female-biased SSD (Hochkirch and Gröning 2008). Most of these instances of SSD are based on total body length as an index of body size, because it is a commonly reported metric of size in the taxonomic literature from which the bulk of these data were gleaned (Hochkirch and Gröning 2008). However, because total body length includes the relatively soft and flexible abdomen that can fluctuate in size, the rate of SSD should be interpreted with caution (Hochkirch and Gröning 2008). Furthermore, because these data rely on a single morphological dimension, conclusions about the extent and direction of SSD are confounded with SShD.

The badlands cricket, *Gryllus personatus* (Uhler 1864), is a mid-sized field cricket (Orthoptera, Gryllinae) inhabiting clay-type badlands in the southwest United States (Weissman and Gray 2019). As typical for most field crickets, males have specialized forewings (tegmina) that they rub together to produce song, and females have a long, thin ovipositor that they use to deposit fertilized eggs into soil (Weissman and Gray 2019). Beyond these sex-limited

Table 1. Selected published descriptions of sexual shape dimorphism in the Orthoptera. Choice of what morphological dimension is considered the focal shape variable and what is considered a reference trait reflects the original publication and is presumably chosen to reflect a functional hypothesis. Obviously, this polarity can be reversed, in which case the direction of dimorphism would be reversed (e.g., female *G. pennsylvanicus* have longer hind femora than males for a given head width; see also figure S2 in Judge and Bonanno 2008).

Taxon	Shape Variable	Reference Trait	Direction	References
Caelifera				
Elasmoderus wagenknechti	forewing length, hindwing length	abdomen length	M>F	Cepeda-Pizarro et al. 2003
Gomphocerus sibiricus	foretibia girth	not specified	M>F	Valverde et al. 2018
Temnomastax spp.	tegmen length	hind femur length	F>M	da Silva Olivier and
	body length	tegmen length	F>M	Aranda 2018
Ensifera				
Acheta domesticus	head width	pronotum width	M>F	Walker et al. 2008
Gryllacropsis sp.	not specified	not specified		Tomar and Diwakar 2020
Gryllus pennsylvanicus	multiple mouthpart dimensions and head width	pronotum length, hind femur length	M>F	Judge and Bonanno 2008
Hemideina crassidens	head length, head width	hind femur length	M>F	Kelly 2006
H. maori	head width	hind tibia length	M>F	Gwynne and Jamieson 1998
Pachyrhamma spp.	length of several antennal sensillae	not specified	various	Fea et al. 2019
P. waitomoensis	hind leg length	pronotum width	M>F	Fea and Holwell 2018
Zaprochiline katydid	auditory bulla size	not specified	F>M	Bailey and Simmons 1991

characteristics, there is no published account of any other sexually dimorphic morphology in the badlands cricket. Our main goal with this study is to test the hypotheses that male and female badlands crickets differ in body size and/or body shape (i.e., display SSD and/or SShD, respectively). We measured four morphological dimensions that are predicted to be sexually dimorphic and then used multivariate statistical methods to assess both SSD and SShD.

Methods

Study animals and care.—Individuals used in this study were the offspring of approximately 60 late instar nymphs (30 males, 30 females) supplied by David Gray (California State University, Northridge) from his laboratory colony of badlands crickets, originally collected from Winslow, Arizona, USA. Crickets were housed in conditions like those described in Judge and Bonanno (2008) at the Department of Biological Sciences, University of Lethbridge. Briefly, hatchlings were added to a large plastic bin (48 cm long, 35 cm wide, 31 cm high) containing layers of egg cartons for shelter, glass shell vials filled with water and stoppered with cotton for moisture, and ground cat food (Iams Original with Chicken; Iams, Mason, Ohio, USA) and ground rabbit food (Martin Little Friends; Martin Mills Inc., Elmira, Ontario, Canada) to provide a variety of food choice (cat food is high in protein, whereas rabbit food is high in fiber). Environmental conditions in the lab during rearing were 25°C, 70% relative humidity, and 12 hours light:12 hours dark daily light cycle. The badlands cricket was to be included in a larger comparative study of aggressive behavior, but this colony had to be euthanized (-20°C for 24 hours) when the study was ended because the second author accepted a fulltime faculty position at MacEwan University. All individuals that were in the colony were preserved separately in 70% ethanol for later measurement.

Measurement of morphology.—We measured five morphological dimensions in all individuals: head width, maxillae span, pronotum length, and both left and right femur length using a methodology similar to that of Judge and Bonanno (2008). Briefly, each individual was removed from their container and dissected to remove the head and both hind femora (at the juncture with the hind coxae) and placed in a standardized position submerged in 70% ethanol under a stereomicroscope (M5; Wild, Heerbrugg, Switzerland) with an attached phototube (Martin Microscope Company, Easley, South Carolina, USA) and digital camera (INFINITY 1-3C; Teledyne Lumenera, Ottawa, Ontario, Canada). We used INFINITY CAPTURE v5.0.2 (Teledyne Lumenera) to capture three images: 1) the ventral head perpendicular to the transverse plane, 2) the dorsal thorax perpendicular to the frontal plane, and 3) the lateral femora perpendicular to the sagittal plane. These photographs were used to place landmarks using the programs tpsUtil and tpsDig2 (SB Morphometrics, https://sbmorphometrics.org/), and the landmarks were converted to linear dimensions using basic trigonometry in Excel (Microsoft Corporation, Redmond, Washington, USA). The landmarks used for each linear dimension are described in detail in Judge and Bonanno (2008, see Fig. 1 therein), and the image capture and morphological measurement procedures are explained in more detail in Dupuis et al. (2020). All photographs and the resulting measurement data used for our analysis are freely available at Dryad (https://doi.org/10.5061/dryad.qjq2bvqkw).

Statistical analysis.—We reduced the number of morphological variables from five to four by using the mean of the left and right femur lengths. Then we used a multivariate general linear model with sex (male or female) as the independent variable and the four morphological variables (head width, maxillae span, pronotum length, and mean femur length) as dependent variables to test for sex-related differences in morphology. Kolmogorov-Smirnov tests were used to assess the normality of the residuals of all statistical analyses. We used IBM SPSS Statistics Version 28.0 (IBM Corporation, Armonk, New York, USA) for all analyses, which were carried out at a Type 1 error rate set at 5%.

Results

The head width, maxillae span, pronotum length, and left and right femur lengths of 167 (71 males and 96 females) adult *G. personatus* were measured. One male was excluded
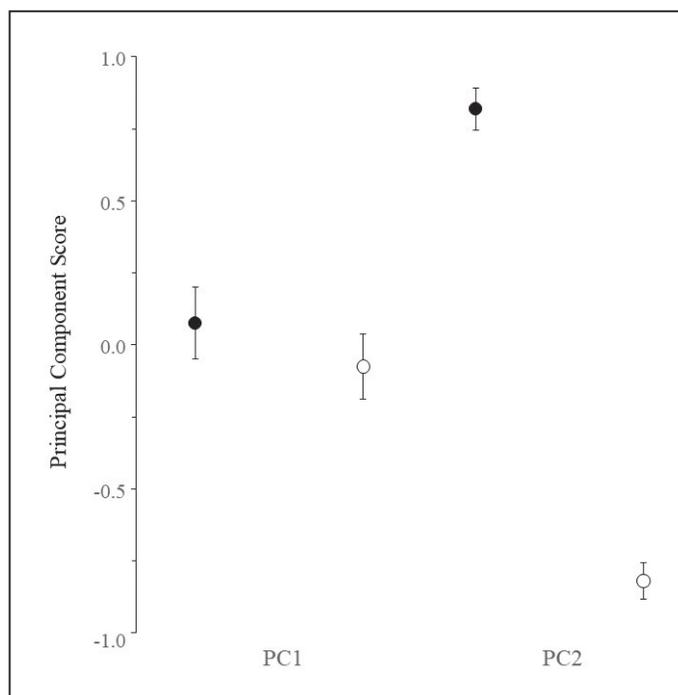
Fig. 1. Average scores for adult male (filled circles) and adult female (open circles) badlands crickets (*Gryllus personatus*) on the first two components from a principal components analysis of the four measured variables: head width, maxillae span, pronotum length, and mean femur length. Error bars represent standard errors. See Table 3 for factor loadings.

from further analysis because he had deformed forewings, and 26 females were excluded using a random number generator to even the sample sizes for males and females at 70 apiece (Table 2). Kolmogorov-Smirnov tests for normality revealed that the residuals from the following statistical tests were normally distributed (all $p > 0.083$). A multivariate GLM with sex as the fixed factor and maxillae span, head width, pronotum length, and mean femur length as dependent variables revealed overall sexual dimorphism ($F_{4,135} = 81.894$, $p < 0.001$), although post-hoc tests showed that the direction of dimorphism depended on the trait measured. Adult males had wider maxillae spans ($F_{1,138} = 54.506$, $p < 0.001$) and wider heads ($F_{1,138} = 10.492$, $p = 0.002$), whereas adult females had longer pronota ($F_{1,138} = 13.587$, $p < 0.001$) and longer femora ($F_{1,138} = 7.217$, $p = 0.008$) (Table 2).

Given that the direction of sexual dimorphism varied across linear dimensions, it was not clear whether males and females

Table 2. Means ± standard deviations (range in parentheses) of five measures of size in the badlands cricket (*Gryllus personatus*). Mean femur length is the average of left and right femora, and geometric mean size is the fourth root of the product of head width, maxillae span, pronotum length, and mean femur length. N = 70 for both males and females.

Measurement (mm)	Males	Females
Maxillae Span	4.87±0.47 (3.87–5.95)	4.38±0.30 (3.58–5.05)
Head Width	5.18±0.39 (4.21–6.06)	4.99±0.33 (4.11–5.85)
Pronotum Length	3.29±0.26 (2.49–3.78)	3.45±0.27 (2.66–3.98)
Mean Femur Length	9.90±0.68 (8.30–11.68)	10.22±0.73 (8.45–12.02)
Geometric Mean Size	5.35±0.40 (4.28–6.26)	5.27±0.36 (4.27–6.13)

Table 3. Results of the principal components analyses for adult badlands crickets (*Gryllus personatus*) including factor loadings, eigenvalues, and percent variance explained for PC1 and PC2.

Dimension	PC1	PC2
Maxillae Span	0.823	0.554
Head Width	0.955	0.247
Pronotum Length	0.843	-0.486
Mean Femur Length	0.912	-0.309
Eigenvalue	3.132	0.699
% Variance Explained	78.311	17.471

were dimorphic in just body shape or in both body shape and overall body size. We investigated sexual dimorphism in overall size by conducting two separate analyses. First, we calculated the geometric mean of the four morphological measures as an index of overall size (Mosimann 1970) and compared males and females using a t-test. Adult *G. personatus* were not sexually dimorphic in geometric mean size (adults: $t_{138} = 1.318$, $p = 0.190$). Second, we conducted a principal components analysis (PCA) to reduce the four measured variables to a limited number of uncorrelated principal components (PCs), where PC1 represents overall size and other PCs represent latent shape variables (Jolicoeur 1963, Cadima and Jolliffe 1996). Although only PC1 had an eigenvalue over 1, we also extracted PC2 (Table 3) because we had an a priori hypothesis regarding shape difference between the sexes. We tested for size and shape sexual dimorphism using separate t-tests. Adult *G. personatus* were dimorphic in PC2 ($t_{138} = 16.961$, $p < 0.001$) but not PC1 ($t_{138} = 0.888$, $p = 0.376$; Fig. 1).

To further explore adult sexual dimorphism, we conducted a discriminant function analysis (DFA) to find out whether there was a linear combination of our measured variables that could accurately predict the sex of individual adult *G. personatus*. The DFA resulted in a significant linear combination of measurements ($\chi^2_4 = 167.489$, $p < 0.001$) that successfully identified the sex of adult *G. personatus* 94.3% (66/70) of the time for females and 91.4% (64/70) of the time for males. The resulting canonical dis-

Table 4. Structure matrix from a discriminant function analysis distinguishing adult male and adult female badlands crickets (*Gryllus personatus*). Values represent the pooled within-groups correlations between discriminating variables and the standardized canonical discriminant function.

Variable	Function
Maxillae Span	0.403
Head Width	0.177
Pronotum Length	-0.201
Mean Femur Length	-0.147

criminant function was positively correlated with head width and maxillae span and negatively correlated with pronotum length and mean femur length (Table 4).

Finally, we wanted to test whether the SShD we detected in lab-reared badlands crickets was generalizable to the species. First, we calculated the ratio of head width to pronotum length. This ratio variable was sexually dimorphic in adults ($t_{138} = 11.520$, $p < 0.001$) and was highly positively correlated with both PC2 ($r = 0.917$, $p < 0.001$) and the discriminant function ($r = 0.821$, $p < 0.001$). To assess the generalizability of this ratio, we used the online natural history website iNaturalist to collect images of wild adult *G. per-*

sonatus and measured the ratio of head width to pronotum length using the same procedure as above. We chose only observations that had 1) at least one photo taken from above and perpendicular to the frontal plane and 2) attained the status of "Research Grade", which meant that at least two people had agreed on the species-level identification with no dissenting opinions. This selection procedure resulted in 10 useable observations (9 females and 1 male). Because of the small sample size, we did not perform a statistical analysis comparing the head width:pronotum length ratios of wild crickets to lab-reared crickets. In wild crickets, as in lab-reared crickets, the male had a bigger ratio than females, and the ratios of wild crickets were less than the ratios of lab-reared crickets, although this difference was less than 5% (Fig. 2).

Discussion

In this study, we tested whether the badlands cricket, *Gryllus personatus*, displayed SSD, SShD, or both. Of the four morphological dimensions that we measured, all were highly positively correlated, and all were sexually dimorphic in adults but in contrasting directions. Adult females had longer hind femora and longer pronota but narrower heads and smaller maxillae spans than adult males (Table 2, Fig. 3), clearly indicating SShD. Because the direction of sexual dimorphism varied by morphological dimension, it was unclear whether badlands crickets were sexually dimorphic in overall body size. We addressed this question in two ways: 1) we compared adult males and females on the geometric mean of all measured variables (GMS), and 2) we used principal components analysis (PCA) to extract a multivariate measure of size (principal component 1, PC1) and an uncorrelated PC2, which can be interpreted as a measure of shape (Jolicoeur 1963). Adult males and females differed on PC2 but not PC1 or GMS, indicating that adult badlands crickets are sexually dimorphic for shape but not size. To further explore SD in the badlands cricket, we conducted a DFA that extracted a linear combination of the measured variables that accurately identified the sex of adult crickets at least 91% of the time. The resulting discriminant function had factor loadings that closely mirrored those of PC2, namely that head width and maxillae span loaded in the opposite direction as pronotum length and mean femur length. These patterns are consistent with the divergent univariate patterns of sexual dimorphism (Table 2) and describe a pattern of SShD whereby adult males have larger heads and mouthparts and adult females have larger thoraxes and hind legs.

Males of many animals have relatively bigger heads and mouthparts than females, including lizards and snakes (e.g., Becker and Paulissen 2012, King et al. 1999, Kratochvíl and Frynta 2002), amphibians (e.g., Katsikaros and Shine 1997, Zhang et al. 2020), fish (e.g., Laporte et al. 2018), mammalian carnivores (e.g., Gittleman and Van Valkenburgh 1997), beetles (e.g., Marlowe et al. 2015). and orthopterans (e.g., Kelly 2006, Walker et al. 2008, Judge and Bonanno 2008) (see Shine 1989 for a review of sexually dimorphic trophic structures). Amongst orthopterans, larger head size in males is thought to be the result of sexual selection because males compete for access to female mates by grappling with their mouthparts (Kelly 2006, Judge and Bonanno 2008). In the fall field cricket, *G. pennsylvanicus*, males with proportionately larger heads were more likely to win aggressive contests, but only if those contests escalated to grappling with mouthparts (Judge and Bonanno 2008). Like most *Gryllus* species (Jang et al. 2008, Bertram et al. 2011), adult male badlands crickets compete aggressively with each other for females using their heads and mouthparts
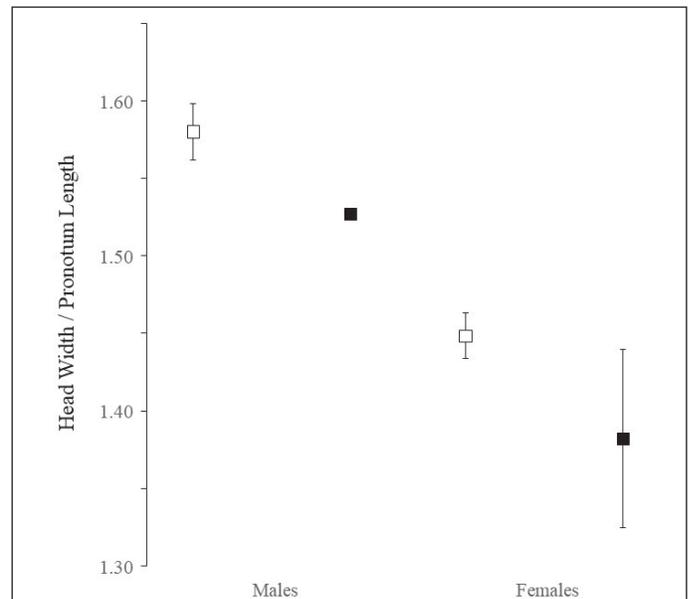

Fig. 2. Average values for the ratio of head width to pronotum length for lab reared (open squares, N = 70 for both sexes) and wild (filled squares, N = 1 male and 9 females) badlands crickets (*Gryllus personatus*). Error bars represent 95% confidence limits for lab reared crickets and ± one standard deviation for wild females.
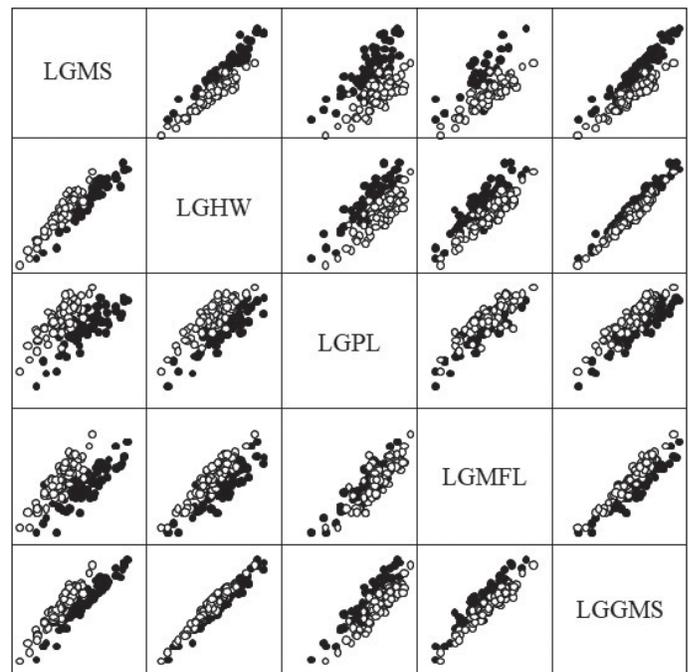

Fig. 3. Matrix scatterplot of the four measured variables: maxillae span (MS), head width (HW), pronotum length (PL) and mean femur length (MFL), and geometric mean size (GMS) for male (filled circles, N = 70) and female (open circles, N = 70) badlands crickets (*Gryllus personatus*). All variables have been log transformed (LG) to facilitate comparison of scaling relationships. Note that the axis labels are all contained along the diagonal so that each is both an x-axis label for any plots above and below and a y-axis label for any plots to the left and right. Thus, every pairwise combination of variables is plotted twice, with each variable appearing on the x-axis on one side of the diagonal and on the y-axis on the other.

Table 5. Studies from a special issue on body size in Orthoptera that measured multiple homologous morphological dimensions in both males and females, where, in principle, it would have been possible to evaluate both SSD and SShD. Columns indicate the taxa studied, the number of morphological dimensions measured, whether SSD was evaluated (and if so whether a univariate or multivariate measure of body size was used), conclusions regarding the direction of SSD, and whether SShD was evaluated.

Taxa	Measurements	SSD?	SSD Pattern	SShD?	Reference
Caelifera					
Chorthippus vagans	4	Yes (U)	F>M	-	Ciplak et al. 2008
Cornops aquaticum	3	Yes (U)	F>M	Yes	Adis et al. 2008
Dactylotum variegatum	2	Yes (U)	F>M	Yes	DeBano et al. 2008
Dichroplus pratensis	6	No	-	Yes	Bidau and Martí 2008b
	6	Yes (U)	F>M	-	Bidau and Martí 2008a
D. vittatus	6	Yes (U)	F>M	-	Bidau and Martí 2008a
Gomphocerinae (8 spp.)	10	Yes (U)	F>M	-	Picaud and Petit 2008
Oedipoda miniata	4	Yes (U)	F>M	-	Ciplak et al. 2008
Oedipodinae (4 spp.)	10	Yes (U)	F>M	-	Picaud and Petit 2008
Podisma sapporensis	8	No	-	-	Sugano et al. 2008
Romalea microptera	2	Yes (U)	F>M	-	Huizenga et al. 2008
	10	Yes (U)	F>M	Yes	Vincent and Lailvaux 2008
Ensifera					
Pholidoptera frivaldskyi	5	Yes (U)	F>M	-	Fabriciusová et al. 2008
Poecilimon birandi	4	Yes (U)	F>M	-	Ciplak et al. 2008
P. thessalicus	3	Yes (U)	F>M	-	Lehmann and Lehmann 2008
Roeseliana roeselii	5	No	-	-	Berggren 2008
Stenopelmatus sp.	4	Yes (U)	No	Yes	Weissman et al. 2008

(D. Gray, pers. comm.), suggesting that the sexual dimorphism in head size relative to pronotum length may also be influenced by sexual selection through male-male competition. Conversely, the observed SShD may also reflect differences between the sexes in mobility, with females evolving longer legs and larger thoraxes (i.e., increase stride length and leg muscle mass, respectively) because sexually active female field crickets search for sedentary singing males (Alexander 1961) all the while attempting to avoid predation, which may be strongly influenced by jumping ability (e.g., Ercit et al. 2014). There are several mechanisms which may result in sex-specific optima for morphological (or other) traits (Shine 1989, Blanckenhorn 2005), and future research should investigate sex-specific mobility patterns, diet, burrow digging, and aggression and the adaptiveness of variation in head and mouthpart size versus thorax and leg size.

Even though every morphological trait we measured in adult badlands crickets was sexually dimorphic in univariate analyses, our multivariate analysis failed to detect any evidence of SSD. This contrasts with the almost universal female-biased SSD in over 1500 species of Orthoptera reported in a recent review (Hochkirch and Gröning 2008). This difference is not surprising given that we used a multivariate approach to measuring body size, whereas, by necessity, Hochkirch and Gröning were constrained to use total body length, a univariate measure of body size that is widely reported in the taxonomic literature that formed the basis of their dataset (Hochkirch and Gröning 2008). We did not measure total body length because of the inherent variability in this measurement due to the effects on abdomen size of nutritional status, oocyte growth, and preservation artefacts (Hochkirch and Gröning 2008), and so our results are not directly comparable. However, our study raises questions as to the true extent of SSD and how often SSD is conflated with SShD. In a recent special issue on body size in Orthoptera (Whitman and Vincent 2008), of 13 studies that measured multiple homologous morphological variables in both males and females (representing 27 species), only 5 evaluated SShD, and all 5 found evidence supporting sex differences in body shape (Adis et al. 2008, Bidau and Martí 2008b, DeBano 2008, Vincent and Lailvaux 2008, Weissman et al. 2008). Furthermore, of the 9 studies that evaluated SSD, all but one concluded that females were larger than males; none used a multivariate measure of size but instead evaluated SSD separately for one or more individual measurements (Table 5). It is unclear whether a multivariate measure of body size would have changed the conclusions of these studies, but until more studies assess both SSD and SShD, we will not know how often these two sexual dimorphisms confound or complement each other.

Although we failed to detect SSD using multivariate methods, the conclusion that adult badlands crickets are not sexually dimorphic for body size should be viewed with some caution as it may depend on the choice of measured dimensions. Choosing an appropriate index of body size is no simple task (Fairbairn 2007), and this is precisely because of shape variation within species, including 1) SShD, 2) polymorphisms (e.g., alternative male morphs in isopods, Shuster 1987), 3) age-related changes in body shape, and 4) condition-dependent effects on body shape (e.g., parasite effects). Many researchers use a single morphological dimension as an index of size (Fairbairn 2007). This practice has the advantage of convenience, standardization, and comparability, whereas multivariate measures of size may not be convenient and can be sample-dependent and therefore not comparable between studies (e.g., principal components). In insects, head width is often used as an index of size (Fairbairn 2007). Because of mounting evidence of relative head size difference between males and females in Orthoptera (e.g., Kelly 2006, Walker et al. 2008, Judge and Bonanno 2008, this study, KAJ unpubl. data) it is becoming increasingly obvious that, for studies of orthopterans where sex is a factor of interest, using head width as an index of body size is no longer appropriate. Failing any consensus on a single measure of size, we recommend a geometric mean of head width, pronotum length, and hind femur length. This measure is 1) multivariate, 2) representative (i.e., the three dimensions represent two body regions

and three morphological axes), 3) convenient (i.e., only three dimensions per individual that can be measured on both live and preserved specimens), 4) universal (i.e., all Orthoptera have these three structures, which is not the case for wings), 5) comparable (i.e., not sample dependent like PC-based size measures), and 6) insensitive to variation in individual condition and damage/preservation artifacts (i.e., does not include weight or dimensions of the abdomen, and component dimensions are rigid and shrink little with drying). Even if individual studies chose to base their analyses on a different index of size, widespread measurement of head width, pronotum length, and hind femur length would greatly facilitate comparative analyses of both SSD and SShD.

SShD variation can be measured in a variety of ways, including intersexual comparisons of 1) regression slopes, 2) second and higher order principal components, 3) values on a discriminant function separating males and females, and 4) ratios of different dimensions to an index of body size (e.g., shape ratios; Mosimann 1970). Ideally SShD studies should incorporate more than one of these methods, and to the extent that different methods result in similar conclusions, shape ratios offer a useful comparative function that is absent from the other multivariate, sample-dependent methods. Ratios are scale-independent and so can be calculated from any image regardless of magnification. In the badlands cricket, results from PCA, DFA, and a simple comparison of the ratio of head width to pronotum length all suggested the same conclusion: that males have relatively wider heads than females. We then used the simple ratio method to measure SShD in a sample of images of badlands crickets posted by citizen scientists to iNaturalist. The head width/pronotum length ratios of these wild crickets were within 5% of the averages of our lab-reared individuals, and the degree of SShD was similar in wild and lab-reared badlands crickets. It is worth noting that machine learning methods for image recognition, such as the one used by iNaturalist to suggest species identification, rely on scale-independent characteristics such as ratios of different dimensions.

In conclusion, we found evidence of SShD in adult badlands crickets: females had relatively longer hind legs and pronota than males, who had relatively wider heads and maxillae spans than females. A variety of multivariate methods failed to detect SSD, and although we cannot (nor wish to) claim that male and female adult badlands crickets are the same size, we do suggest that our results are cause to revise how body size is typically measured in arthropods in general and Orthoptera in particular. The geometric mean of three body dimensions—head capsule width, pronotum length, and hind femur length—has both the properties of universality, sample independence, comparability, and is multivariate. The widespread adoption of this body size measurement by orthopterists would open up enormous possibilities for comparative assessments of the prevalence and direction of both SSD and SShD.

Acknowledgements

References

Adis J, Sperber CF, Brede EG, Capello S, Franceschini MC, Hill M, Lhano MG, Marques MM, Nunes AL, Polar P (2008) Morphometric differences in the grasshopper *Cornops aquaticum* (Bruner, 1906) from South America and South Africa. Journal of Orthoptera Research 17: 141–147. https://doi.org/10.1665/1082-6467-17.2.141

Alexander RD (1961) Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). Behavior 17: 130–223. https://doi.org/10.1163/156853961X00042

Andersson M (1994) Sexual Selection. Princeton University Press, Princeton, 599 pp.

Bagchi B, Corbel Q, Khan I, Payne E, Banerji D, Liljestrand-Rönn J, Martinossi-Allibert I, Baur J, Sayadi A, Immonen E, Arnqvist G, Söderhäll I, Berger D (2021) Sexual conflict drives micro- and macroevolution of sexual dimorphism in immunity. BMC Biology 19, 114: 19 pp. https://doi.org/10.1186/s12915-021-01049-6

Bailey WJ, Simmons LW (1991) Male-male behavior and sexual dimorphism of the ear of a zaprochiline tettigoniid (Orthoptera: Tettigoniidae). Journal of Insect Behavior 4: 51–65. https://doi.org/10.1007/BF01092551

Becker BM, Paulissen MA (2012) Sexual dimorphism in head size in the little brown skink (*Scincella lateralis*). Herpetological Conservation and Biology 7: 109–114.

Berggren Å (2008) The effects of population and landscape ecology on body size in orthopterans. Journal of Orthoptera Research 17: 183–188. https://doi.org/10.1665/1082-6467-17.2.183

Bertram SM, Rook VLM, Fitzsimmons JM, Fitzsimmons LP (2011) Fine- and broad-scale approaches to understanding the evolution of aggression in crickets. Ethology 117: 1067–1080. https://doi.org/10.1111/j.1439-0310.2011.01970.x

Bidau CJ, Martí DA (2008a) Contrasting patterns of sexual size dimorphism in the grasshoppers *Dichroplus vittatus* and *D. pratensis* (Acrididae, Melanoplinae). Journal of Orthoptera Research 17: 201–211. https://doi.org/10.1665/1082-6467-17.2.201

Bidau CJ, Martí DA (2008b) Geographic and climatic factors related to a body-size cline in *Dichroplus pratensis* Bruner, 1900 (Acrididae, Melanoplinae). Journal of Orthoptera Research 17: 149–156. https://doi.org/10.1665/1082-6467-17.2.149

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

Cadima JFCL, Jolliffe IT (1996) Size- and shape-related principal component analysis. Biometrics 52: 710–716. https://doi.org/10.2307/2532909

Cepeda-Pizarro J, Vega S, Vásquez H, Elgueta M (2003) Morfometría y dimorfismo sexual de *Elasmoderus wagenknechti* (Liebermann) (Orthoptera: Tristiridae) en dos eventos de irrupción poblacional. Revista Chilena de Historia Natural 76: 417–435. https://doi.org/10.4067/S0716-078X2003000300007

Ciplak B, Sirin D, Taylan MS, Kaya S (2008) Altitudinal size clines, species richness and population density: case studies in Orthoptera. Journal of Orthoptera Research 17: 157–163. https://doi.org/10.1665/1082-6467-17.2.157

da Silva Olivier R, Aranda R (2018) Are anatomical measurements useful for interspecific and sexual differentiation of *Temnomastax* (Orthoptera: Eumastacidae) species? Zoological Science 35: 268–275. https://doi.org/10.2108/zs170088

Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London, 475 pp. https://doi.org/10.5962/bhl.title.2092

DeBano SJ (2008) Morphometric condition as a measure of energetic content and reproductive potential in *Dactylotum variegatum*. Journal of Orthoptera Research 17: 293–300. https://doi.org/10.1665/1082-6467-17.2.293

Dupuis JR, Judge KA, Brunet BMT, Ohlmann Chan S, Sperling FAH (2020) Does hunger lead to hybridization in a genus of sexually cannibalistic insects (Orthoptera: Prophalangopsidae)? Biological Journal of the Linnean Society 131: 434–448. https://doi.org/10.1093/biolinnean/blaa094

Ercit K, Martinez-Novoa A, Gwynne DT (2014) Egg load decreases mobility and increases predation risk in female black-horned tree crickets (*Oecanthus nigricornis*). PLoS ONE 9: e110298. https://doi.org/10.1371/journal.pone.0110298

Esperk T, Tammaru T, Nylin S, Teder T (2007) Achieving high sexual size dimorphism in insects: females add instars. Ecological Entomology 32: 243–256. https://doi.org/10.1111/j.1365-2311.2007.00872.x

Fairbairn DJ (2007) Introduction: the enigma of sexual size dimorphism. In: Fairbairn DJ, Blanckenhorn WU, Székely T (Eds) Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, Oxford, 1–10. https://doi.org/10.1093/acprof:oso/9780199208784.003.0001

Fairbairn DJ, Blanckenhorn WU, Székely T (2007) Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, Oxford, 266 pp. https://doi.org/10.1093/acprof:oso/9780199208784.001.0001

Fabriciusová V, Kaňuch P, Krištín A (2008) Body size patterns of *Pholidoptera frivaldskyi* (Orthoptera) in very isolated populations. Journal of Orthoptera Research 17: 171–176. https://doi.org/10.1665/1082-6467-17.2.171

Fea M, Holwell GI (2018) Exaggerated male legs increase mating success by reducing disturbance to females in the cave wētā *Pachyrhamma waitomoensis*. Proceedings of the Royal Society of London B 285: 20180401. https://doi.org/10.1098/rspb.2018.0401

Fea MP, Mark CJ, Holwell GI (2019) Sexually dimorphic antennal structures of New Zealand cave wētā (Orthoptera: Rhaphidophoridae). New Zealand Journal of Zoology 46: 124–148. https://doi.org/10.1080/03014223.2018.1520266

Foellmer MW, Moya-Laraño J (2007) SSD in spiders: patterns and processes. In: Fairbairn DJ, Blanckenhorn WU, Székely T (Eds) Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, Oxford, 71–81. https://doi.org/10.1093/acprof:oso/9780199208784.003.0008

Gittleman JL, Van Valkenburgh B (1997) Sexual dimorphism in the canines and skulls of carnivores: Effects of size, phylogeny, and behavioural ecology. Journal of Zoology 242: 97–117. https://doi.org/10.1111/j.1469-7998.1997.tb02932.x

Gwynne DT, Jamieson I (1998) Sexual selection and sexual dimorphism in a harem-polygynous insect, the alpine weta (*Hemideina maori*, Orthoptera Stenopelmatidae). Ethology, Ecology and Evolution 10: 393–402. https://doi.org/10.1080/08927014.1998.9522852

Herberstein ME, Painting CJ, Holwell GI (2017) Scramble competition polygyny in terrestrial arthropods. Advances in the Study of Behavior 49: 237–295. https://doi.org/10.1016/bs.asb.2017.01.001

Hochkirch A, Gröning J (2008) Sexual size dimorphism in Orthoptera (sens. str.) – a review. Journal of Orthoptera Research 17: 189–196. https://doi.org/10.1665/1082-6467-17.2.189

Hopkins BR, Kopp A (2021) Evolution of sexual development and sexual dimorphism in insects. Current Opinion in Genetics and Development 69: 129–139. https://doi.org/10.1016/j.gde.2021.02.011

Huizenga KM, Shaidle MD, Brinton JS, Gore LA, Ebo MA, Solliday AJ, Buguey PJ, Whitman DW, Juliano SA (2008) Geographic differences in the body sizes of adult *Romalea microptera*. Journal of Orthoptera Research 17: 135–139. https://doi.org/10.1665/1082-6467-17.2.135

Jang Y, Gerhardt HC, Choe JC (2008) A comparative study of aggressiveness in eastern North American field cricket species (genus *Gryllus*). Behavioral Ecology and Sociobiology 62: 1397–1407. https://doi.org/10.1007/s00265-008-0568-6

Jolicoeur P (1963) The multivariate generalization of the allometry equation. Biometrics, 19: 497–499. https://doi.org/10.2307/2527939

Judge KA, Bonanno VL (2008) Male weaponry in a fighting cricket. PLoS ONE 3(12): e3980. https://doi.org/10.1371/journal.pone.0003980

Katsikaros K, Shine R (2006) Sexual dimorphism in the tusked frog, *Adelotus brevis* (Anura: Myobatrachidae): the roles of natural and sexual selection. Biological Journal of the Linnean Society 60: 39–51. https://doi.org/10.1111/j.1095-8312.1997.tb01482.x

Kelly CD (2006) Fighting for harems: assessment strategies during male–male contests in the sexually dimorphic Wellington tree weta.

Animal Behaviour 72: 727–736. https://doi.org/10.1016/j.anbehav.2006.02.007

Kelly CD, Stoehr AM, Nunn C, Smyth KN, Prokop ZM (2018) Sexual dimorphism in immunity across animals: a meta-analysis. Ecology Letters 21: 1885–1894. https://doi.org/10.1111/ele.13164

King RB, Bittner TD, Queral-Regil A, Cline JH (1999) Sexual dimorphism in neonate and adult snakes. Journal of Zoology, London 247: 19–28. https://doi.org/10.1111/j.1469-7998.1999.tb00189.x

Kokko H, Jennions MD (2008) Parental investment, sexual selection and sex ratios. Journal of Evolutionary Biology 21: 919–948. https://doi.org/10.1111/j.1420-9101.2008.01540.x

Kratochvíl L, Frynta D (2002) Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). Biological Journal of the Linnean Society 76: 303–314. https://doi.org/10.1111/j.1095-8312.2002.tb02089.x

Laporte M, Berrebi P, Claude J, Vinyoles D, Pou-Rovira Q, Raymond J-C, Magnan P (2018) The ecology of sexual dimorphism in size and shape of the freshwater blenny *Salaria fluviatilis*. Current Zoology 64: 183–191. https://doi.org/10.1093/cz/zox043

Lehmann GUC, Lehmann AW (2008) Variation in body size among populations of the bushcricket *Poecilimon thessalicus* (Orthoptera: Phaneropteridae): an ecological adaptation. Journal of Orthoptera Research 17: 165–169. https://doi.org/10.1665/1082-6467-17.2.165

Marlowe MH, Murphy CA, Chatzimanolis S (2015) Sexual dimorphism and allometry in the sphecophilous rove beetle *Triacrus dilatus*. PeerJ 3: e1123. https://doi.org/10.7717/peerj.1123

Martins MJF, Hunt G, Thompson CM, Lockwood R, Swaddle JP, Puckett TM (2020) Shifts in sexual dimorphism across a mass extinction in ostracods: implications for sexual selection as a factor in extinction risk. Proceedings of the Royal Society B 287: 20200730. https://doi.org/10.1098/rspb.2020.0730

Mosimann JE (1970) Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. Journal of the American Statistical Association 65: 930–945. https://doi.org/10.1080/01621459.1970.10481136

Picaud F, Petit DP (2008) Body size, sexual dimorphism and ecological succession in grasshoppers. Journal of Orthoptera Research 17: 177–181. https://doi.org/10.1665/1082-6467-17.2.177

Selander RK (1966) Sexual dimorphism and differential niche utilization in birds. Condor 68: 113–151. https://doi.org/10.2307/1365712

Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. The Quarterly Review of Biology 64: 419–461. https://doi.org/10.1086/416458

Shuster SM (1987) Alternative reproductive behaviors: three discrete male morphs in *Paracerceis sculpta*, an intertidal isopod from the northern Gulf of California. Journal of Crustacean Biology 7: 318–327. https://doi.org/10.1163/193724087X00270

Stillwell RC, Blanckenhorn WU, Teder T, Davidowitz G, Fox CW (2010) Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: from physiology to evolution. Annual Review of Entomology 55: 227–245. https://doi.org/10.1146/annurev-ento-112408-085500

Sugano YC, Sasaki Y, Akimoto S (2008) Effects of body size and shape on mating frequency in the brachypterous grasshopper *Podisma sapporensis*. Journal of Orthoptera Research 17: 243–248. https://doi.org/10.1665/1082-6467-17.2.243

Tomar M, Diwakar S (2020) Investigating host plant association, calling activity, and sexual dimorphism in Indian *Gryllacropsis* sp. (Orthoptera: Anostostomatidae). Ecology and Evolution 10: 11850–11860. https://doi.org/10.1002/ece3.6819

Uhler PR (1864) Orthopterological contributions. Proceedings of the Entomological Society of Philadelphia 2: 543–555. https://biostor.org/reference/69335

Valverde JP, Eggert H, Kurtz J, Schielzeth H (2018) Condition-dependence and sexual ornamentation: Effects of immune challenges on a highly sexually dimorphic grasshopper. Insect Science 25: 617–630. https://doi.org/10.1111/1744-7917.12448

Vincent SE, Lailvaux SP (2008) Does phenotypic integration constrain sexual size dimorphism in eastern lubber grasshoppers (*Romalea microptera*)? Journal of Orthoptera Research 17: 219–225. https://doi.org/10.1665/1082-6467-17.2.219

Walker SE, Roberts JA, Adame I, Collins CJ, Lim D (2008) Heads up: sexual dimorphism in house crickets (*Acheta domesticus*). Canadian Journal of Zoology 86: 253–259. https://doi.org/10.1139/Z08-001

Weissman DB, Gray DA (2019) Crickets of the genus *Gryllus* in the United States (Orthoptera: Gryllidae: Gryllinae). Zootaxa 4705: 1–277. https://doi.org/10.11646/zootaxa.4705.1.1

Weissman DB, Judge KA, Williams SC, Whitman DW, Lee VF (2008) Small-male mating advantage in a species of Jerusalem cricket (Orthoptera: Stenopelmatinae: *Stenopelmatus*). Journal of Orthoptera Research 17: 321–332. https://doi.org/10.1665/1082-6467-17.2.321

Whitman DW (2008) The significance of body size in the Orthoptera: a review. Journal of Orthoptera Research 17: 117–134. https://doi.org/10.1665/1082-6467-17.2.117

Whitman DW, Vincent S (2008) Body size in Orthoptera: Preface. Journal of Orthoptera Research 17: 113–114. https://doi.org/10.1665/1082-6467-17.2.113

Zhang L, Sheng Y, Yuan X, Yu F, Zhong X, Chen X (2020) Sexual dimorphism in *Scutiger boulengeri*, an endemic toad from the Tibetan Plateau. Animal Biology 70: 445–457. https://doi.org/10.1163/15707563-bja10041