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Sexual size and shape dimorphism are consistent with predictions that both natural and sexual selection are driving the evolution of sexual dimorphism in Mormon crickets, *Anabrus simplex*

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Abstract

Background Selection can be a powerful force causing morphological adaptation in populations. We tested predictions about the role of both natural and sexual selection in shaping morphology in the Mormon cricket, *Anabrus simplex*, a species with two population types that differ in their ecological conditions. Solitary populations are characterized by low densities, non-migratory individuals, and typical mating roles (males compete for access to choosy females), whereas gregarious populations are characterized by high densities, migratory behaviour, reversed mating roles, and widespread cannibalism. We collected individuals from both solitary and gregarious populations– characterized by their behaviour and not morphology– and measured several morphological traits. We transformed these traits to shape variables by dividing each measurement by a geometric mean of several metric dimensions representing body size. We tested for population type and sex differences in size and shape variables, and we tested for population type differences in several sex-limited shape variables. We also used discriminant function analysis to test whether a previously enigmatic population, found to be genetically like gregarious populations, but exhibiting many aspects of solitary population behaviour, was morphologically more like solitary or gregarious populations. Our analysis was used to determine the minimum number of measurements needed to assign specimens to the correct population type.

Results We found that gregarious populations were larger in body size than solitary populations and that females were larger than males in both population types. This sexual size dimorphism was more pronounced in solitary populations. Solitary and gregarious populations displayed several other shape differences as well as differences in the degree of sexual dimorphism in shape. The enigmatic population was unambiguously classified as morphologically more like gregarious populations, a finding which agrees with previous work showing genetic

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similarities with gregarious populations. Head width was consistently the best character to distinguish members of both populations.

Conclusions Patterns of sexual size and shape dimorphism are consistent with predictions that both natural and sexual selection are driving the evolution of sexual dimorphism in Mormon crickets. Future work should measure the direction and shape of selection on both males and females in solitary and gregarious populations, focusing particular attention on head shape.

Keywords Sexual size dimorphism, Sexual selection, Natural selection, Cannibalism, Shape ratio, Orthoptera

Background

Sexual dimorphism in both size (SSD) and shape (SShD) are common across sexually reproducing organisms [1–3]. The causes of these dimorphisms have been debated ever since Darwin [2, 4–7]. Darwin originally recognized that both sexual and natural selection could result in sexual dimorphism [1]. And although the subsequent literature has tended to categorize mechanisms generating sexual dimorphism differently [4, 5, 7–9], all explanations rely on sexual selection, natural selection, or both [6]. Comparative studies have been used extensively to test factors that influence sexual dimorphism (reviewed in [6], [10]), however species where mating roles (i.e., prior to copulation, which sex is more competitive for, or more choosy among, mates) and selective pressures vary among populations offer an alternative means to test hypotheses concerning the evolution of sexual dimorphism [11–13].

Mating-role plasticity among populations is known in insects when females receive a nutritious male food gift, with mating role reversal occurring when hungry females supplement their diet by mating more frequently [14–16]. In some species of katydids (Orthoptera; Tettigoniidae) this increase in the relative value of the food gift can cause females to compete for access to males and males to become choosier among prospective mates. Thus, when food is plentiful, sexual selection is likely stronger on males than females, whereas the reverse may be true when food is scarce [15, 17–19].

In systems with mating gifts, natural selection pressures also likely vary with food availability. For example, there may be greater predation on males that, when food is plentiful, must display or search more to find mates. However, females may be more vulnerable to predation when food is scarce as they search more for gift giving males [20, 21]. In insects with nuptial feeding, variation in the strength and direction of natural selection could select for different degrees of sexual dimorphism. Leimar et al. [22] proposed that, when females are larger than males due to fecundity selection, starved nymphal females can afford to reduce their investment in body size relative to males because, as adults they can acquire resources by mating with males [22, 23].

Mormon crickets (*Anabrus simplex*) are large, flightless katydids (Orthoptera, Tettigoniidae) common across much of western North America [24–26]. Males transfer a large, nutritious spermatophylax (part of the spermatophore) to females during mating which females then consume [27]. Mormon crickets are found in two forms: (1) a smaller "solitary" morph that lives in low-density, stationary populations with plentiful food resources primarily on the east side of the Rocky Mountains, and (2) a larger "gregarious" morph that lives in high-density, migratory bands, generally found on the west side of the Rocky Mountains [17, 28]. Individuals in solitary populations display typical mating roles with males singing to attract choosy females [17]. In gregarious populations, however, individuals are often starved for protein and salt and readily cannibalize conspecifics [29]. As a result of this nutrient deprivation, the value of the male spermatophylax increases [18], the mating roles are reversed with females competing aggressively for matings [27] and males, who sing less than in solitary populations [30], exerting choice for larger, more fecund females [17, 18, 27]. Therefore, environmental differences between the population types seem to produce different natural and sexual selection regimes, which in turn, would be expected to cause differences in morphology.

The present study has four goals. First, the divergent selection regimes operating in solitary and gregarious populations provide us with an opportunity to test several predictions regarding the evolution of SSD and SShD as well as dimorphisms related to population type (Table 1). We categorize our predictions as arising from either natural selection, sexual selection, or both. Sexual selection is that arising out of the competition for mates and fertilizations [1, 31–33]. For example, between members of the competing sex, the sizes of mouthparts and heads might be important in contests over access to mates [34, 35] and in males, paired abdominal appendages called cerci (singular: cercus) function in holding on to mates and prolonging copulation [36]. Natural selection is that arising out of survival needs and/or competition for food ([31], i.e., "narrow sense" natural selection, [37]). For example, given potential selection for cannibalism [29], the size of heads and mouthparts are expected to be relatively larger in both sexes from high-density

Table 1 Predictions regarding the direction of differences in body size (geometric mean of maxillae span, head width, pronotum length and femur length) and shape ratio (SR = length of morphological dimension to body size ratio) between population types (solitary: S and gregarious: G) and sexes (male: M and female: F) in Mormon crickets, *Anabrus simplex*, and whether support was found (Yes or No) in the present study (see text for results of statistical analyses). Sexual selection predictions depend on a significant interaction between population type and sex, so a predicted inequality in one population type is assumed to be greater than in the other population type. See text and Fig. 1 for description of morphological traits

Trait	Selection	Prediction	Rationale	Support	
				NS	SS
Body Size					
	Natural	G > S	selection for cannibalism in G [29]	Y	
		F > M	fecundity selection, but less in G due to female compensatory mating [22]	Y	
	Sexual	GF > GM	F-F fighting in G [17, 18]		N
		SF > SM	F-F scramble competition in G [e.g., 40]		Y
		GF > GM	[30] due to M-M fighting in S [41]		N
Maxillae Span SR					
	Natural	G > S	selection for cannibalism in G [29]	N	
		F > M	increased energy demands of developing eggs as well as preference for larger and thicker foliage [44]	Y	
	Sexual	GF > GM	F-F fighting in G [34]		N
		SM > SF	M-M fighting in S [34]		N
Head Width SR					
	Natural	G > S	selection for cannibalism in G [29]	N	
		F > M	increased energy demands of developing eggs as well as preference for larger and thicker foliage [44]	Y	
	Sexual	GF > GM	F-F fighting in G [34]		N
		SM > SF	M-M fighting in S [34]		N
Pronotum Length SR					
	Natural	G > S	increased thoracic muscles for migration in G [29, 42]	N	
		F > M	increased thoracic muscles to support larger abdomen	N	
	Sexual	SM > SF	increased M calling in S [28] coupled with adaptation of the pronotum to amplify sound [43]		Y
Hind Femur Length SR					
	Natural	G > S	selection for increased mobility during migration in G [29, 42]	N	
		F > M	to support larger abdomen due to fecundity selection	Y	
	Sexual	GF > GM	F-F scramble competition and/or F-F fighting in G [F kick each other in fights: DTG pers. obs.]	N	
		SM > SF	M-M scramble competition and/or M-M fighting in S		N
Male Cercus SRs					
	Sexual	G > S	selection for efficient copulation [i.e., lock-and-key hypothesis: 45] since G are larger than S [DTG pers. obs.]	N	
		S > G	increased F reluctance to mate in S [17, 36]		Y
Female Ovipositor Length SR					
	Natural	S > G	selection for increased mobility in G and/or need for deeper egg placement in higher altitude, wetter sites in S	Y	

gregarious populations compared to low-density solitary populations (e.g., [38]). Second, there are conflicting results on sexual dimorphism in *A. simplex*. Gwynne [17] found that females had longer pronota than males in gregarious but not solitary populations, and Bailey et al. [30] found females to have larger pronota than males' in solitary but not gregarious populations. We hope to clarify the morphological relationships between solitary and gregarious *A. simplex* by measuring more dimensions on a larger sample of individuals from a greater number of populations. Third, we use morphology to classify an enigmatic population at Little Brush Creek in Utah as solitary or gregarious. This population was previously classified as solitary based on lack of migratory behaviour and apparent competition among males [DTG pers. obs.], but which is more like gregarious populations in both genotype and the structure of calling song [30, 39]. Fourth, we ask what minimum set of morphological measurements could be used to accurately distinguish individuals as either solitary or gregarious, which could be useful to managers in identifying locations of potential future outbreaks of gregarious individuals, which are pests [24, 25].

To test for body size and shape differences in Mormon crickets, we measured a number of linear morphological dimensions on males and females from both solitary and gregarious populations. We estimated each individual's body size as the geometric mean of four metric traits common to both males and females. Then we converted each individual measurement to a shape ratio by dividing each value by the individual's body size estimate [46]. Shape ratios are rarely used in evolutionary ecology studies, likely because authors are mainly interested in either "controlling for" body size or examining the allometric relationships between two structures. However, shape ratios are simple descriptors of body shape [46, 47] and are not intended to be used to control body size as in ANCOVA [48]. In addition, shape ratios have advantages over size-corrected residuals because ratios, unlike residuals, are stable properties of the individual and are not subject to change as a function of the comparative sample [49, 50].

Methods

Sample collection

In June and July of 1999, two of us (PDL and DTG) collected 505 adult *A. simplex* (248 males, 257 females) from 12 different populations located throughout the states of Utah and Colorado, USA (Table 2). Populations were classified as either solitary or gregarious based on observations of behaviour and density [27], where solitary populations were low-density ($\leq 3/m^2$), stationary, and exhibited typical mating roles, and gregarious populations were high-density ($> 3/m^2$), migratory and exhibited mating-role reversal. While some individuals in migratory populations may not move as much due to age or temperature [51], migratory behaviour is distinguished from stationary by daily movements of at least some individuals in migratory populations moving greater than 100 m, with some moving up to 2 km in 24 h. Previous work suggested that one of our populations classified as solitary, Little Brush Creek (LBC), is genetically and acoustically more like gregarious populations [30, 39], and preliminary observations of morphology suggested that they were also morphologically more like gregarious populations. For these reasons, we exclude LBC individuals from tests for morphological differences between gregarious and solitary populations, however we later ask the question of whether LBC is morphologically more like gregarious or solitary populations.

Table 2 Numbers of male and female Mormon crickets, *A. simplex*, collected in 1999 from eight solitary and four gregarious populations located in the States of Utah (UT) and Colorado (CO)

Population Type Location	Males	Females
Solitary		
Crested Butte, CO	4	3
Great Sand Dunes, CO	5	3
Indian Meadows, CO	15	2
Kelly Flats, CO	39	21
Little Brush Creek, UT*	12	7
Mosca Pass, CO	3	0
Santa Maria, CO	7	0
Stove Prairie, CO	4	4
Gregarious		
Echo Park Road, CO	28	56
Vernon, Forest, UT	51	72
Vernon, Road, UT	40	42
Dinosaur Park Road, CO	40	47

* Individuals from this population were omitted from correlation analyses and the analysis of population type differences (see text for explanation)

Insects were killed in 1999 by freezing at -20 C and then preserved in 95% ethanol in 2005 for measurement of morphology.

Measurement of morphology

A suite of morphological measurements, predicted to be either naturally selected, sexually selected, or both (Table 1) were taken on all individuals (Fig. 1): (1) maxillae span (distance between the cardo-stipes articulation on the left and right maxillae), (2) head width (maximum width of the head capsule excluding the eyes), (3) pronotum length (distance between the anterior lateral margin of the pronotum to the posterior tip, measured from both the left and right side and averaged), and (4) femur length (maximum distance measured on both left and right hind femora and averaged, if both were available). Additional measurements were taken on males only: three dimensions of both the left and right cerci: (1) cercus length (straight line distance from distal tip to base of cercus), (2) cercus width (distance from secondary tip to base of cercus), and (3) hook length (length of distal tip of cercus; Fig. 1), or females only: ovipositor length (straight line distance from the tip to the base of the ovipositor). Morphological traits were measured from digital camera (Javelin JE-3662HR) images taken from a stereomicroscope using the program NIH Image (National Institute of Health, http://rsb.info.nih.gov/nih-image/). The image resolution for all dimensions was 39 pixels/mm, except for male genital traits, where the resolution was 154 pixels/mm. All measurements were done by lab personnel who were blind to the specific hypotheses being tested, and measurement repeatability was approximately 95% [KAJ unpubl. data].

Differences between solitary and gregarious populations

For comparisons of morphological shape between males and females, and between gregarious and solitary Mormon crickets, we calculated shape ratios [46] by dividing each measurement by an individual's body size estimate. We used the geometric mean of the four traits measured for all individuals (maxillae span, head width, pronotum length and femur length) as our measure of body size.

To test for size and shape differences according to sex and population type, we conducted univariate general linear mixed effects models (GLMM) with sex, population type and their interaction as fixed independent variables, location as a random factor, and either body size or the shape ratios of maxillae span, head width, pronotum

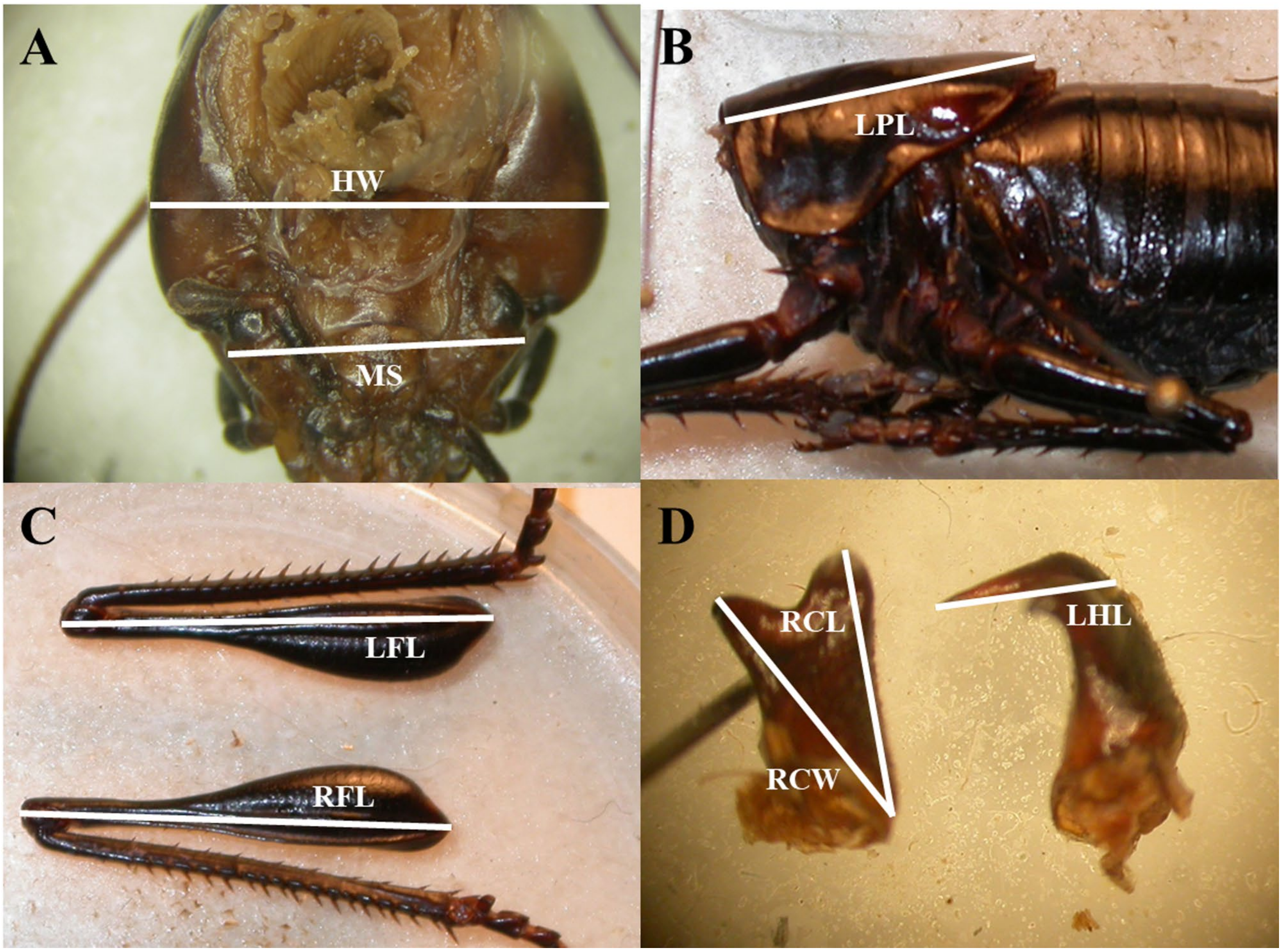

Fig. 1 Morphological measurements taken on individual Mormon crickets, *Anabrus simplex*: (**A**) head width (HW) and maxillae span (MS), (**B**) pronotum length (PL; note left PL shown), (**C**) left and right femur length (LFL, RFL), (**D**) cercus length (CL), cercus width (CW) and hook length (HL). Ovipositor length not shown. PL shown from the left side, CL and CW shown on the right cercus, and HL shown on the left cercus, but measured for both left and right and averaged in all cases

length and femur length as the dependent variable. To test for further shape differences between gregarious and solitary populations in sex-specific traits, we conducted univariate GLMMs separately for males and females with population type as the independent variable, location as a random factor, and the shape ratios of cercus length, cercus width and hook length for males, and ovipositor length shape ratio for females as the dependent variable.

Is the Little Brush Creek population more like solitary or gregarious populations?

To test whether Little Brush Creek (LBC) specimens are more similar morphologically to individuals from solitary or gregarious populations, we conducted a discriminant function analysis (DFA) on the solitary and gregarious populations, excluding LBC, and then used the discriminant function to assign individuals from LBC to either solitary or gregarious population types (i.e., cross-validation analysis). We conducted analyses on males and females separately to allow us to utilize all sex-specific morphological measurements. Both DFAs included the measured traits common to all individuals (maxillae span, head width, pronotum length, femur length). The DFA for males also included cercus traits (cercus length, cercus width and hook length), and the female DFA included ovipositor length.

Distinguishing solitary and gregarious individuals in the field

We conducted backwards stepwise DFAs (i.e., starting with the full complement of traits and progressively eliminating those that failed to improve discrimination) to identify the minimum set of morphological measurements that could be used to distinguish solitary and gregarious individuals. As above, we conducted analyses on males and females separately.

Statistical analysis

All statistical analyses were carried out in IBM SPSS Version 28, except for the mixed effects models, which were conducted using R Version 4.3.2. The dataset and R scripts are freely available at Dryad.

Results

All raw morphological traits (descriptive statistics given in Supplementary Table 1) were positively correlated within each sex and population type combination (Supplementary Table 2). After conversion to shape ratios by dividing each measurement by the geometric mean, many pairwise correlations were no longer statistically significant, and many were negatively correlated (Supplementary Table 3).

Differences between solitary and gregarious populations

Body size

Univariate GLMM revealed a significant interaction between sex and population type in their effects on geometric mean size ($F_{1,\ 481.12} = 16.825$, $p < 0.001$). Because of this statistically significant interaction effect [52], we conducted GLMMs for: (1) solitary and gregarious populations separately to test for sexual dimorphism, and (2) males and females separately to test for population differences. Female Mormon crickets were larger in body size than males in both solitary ($F_{1,\ 106.21} = 96.361$, $p < 0.001$) and gregarious populations ($F_{1,\ 371.13} = 128.57$, $p < 0.001$) although the difference was more pronounced in solitary populations (Fig. 2). Gregarious Mormon crickets were larger in body size than solitary Mormon crickets in both males ($F_{1,9.16} = 52.421$, $p < 0.001$) and females ($F_{1,7.07} = 24.362$, $p = 0.002$) although the difference was greater in males (Fig. 2).

Maxillae span shape ratio

There was no statistically significant effect of the interaction between sex and population type on maxillae span shape ratio ($F_{1,\ 480.70} = 2.050$, $p = 0.153$). After removing the sex by population type interaction, females had larger maxillae span SR than males ($F_{1,\ 475.91} = 6.330$, $p = 0.012$) and gregarious Mormon crickets had larger maxillae span SRs than solitary Mormon crickets, although this difference was not statistically significant ($F_{1,\ 7.39} = 2.946$, $p = 0.128$; Fig. 3A).

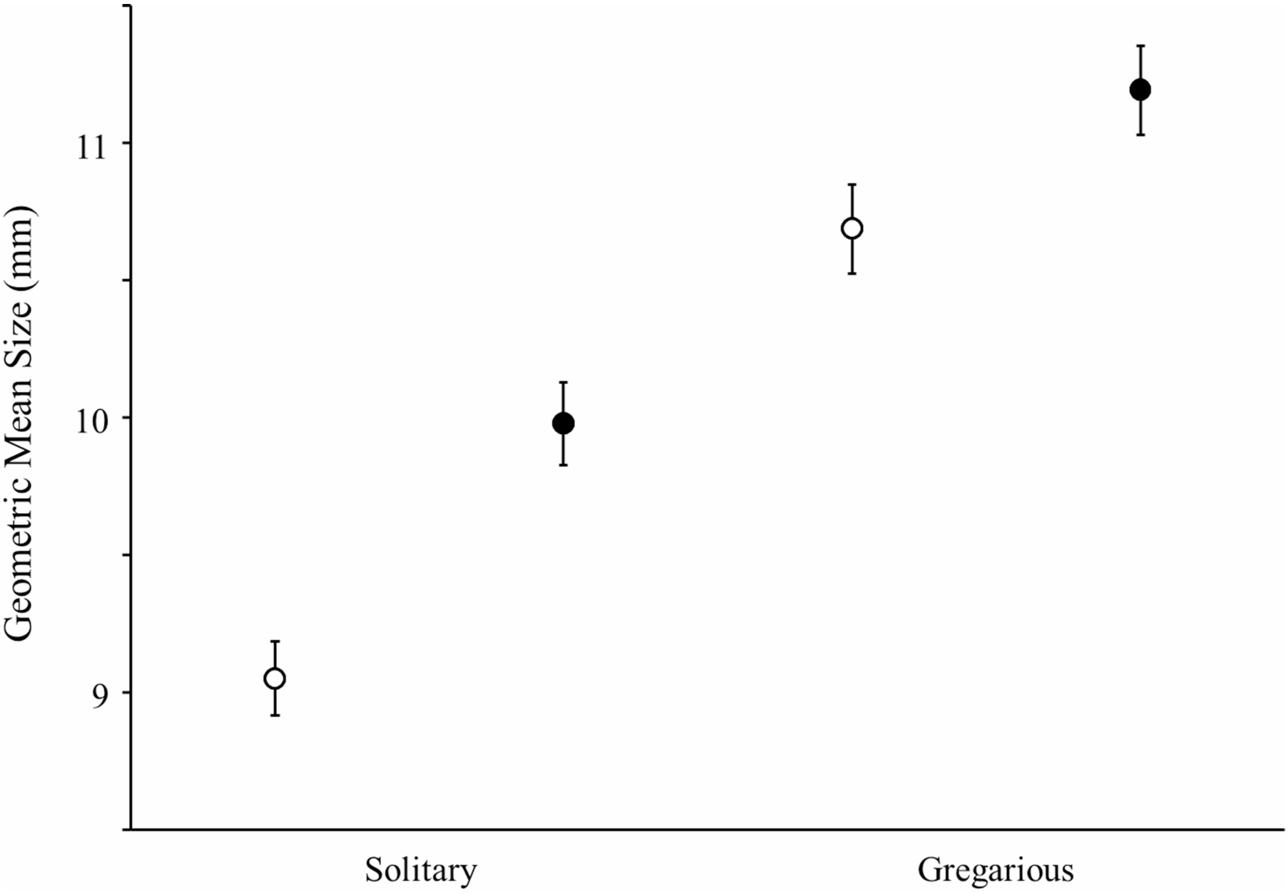

Fig. 2 Geometric mean size for male (open circles) and female (closed circles) Mormon crickets, *Anabrus simplex*, from both gregarious (G) and solitary (S) populations. Bars represent ± 1 SEM. Values are estimated marginal means from a linear mixed model. See text for statistically significant differences

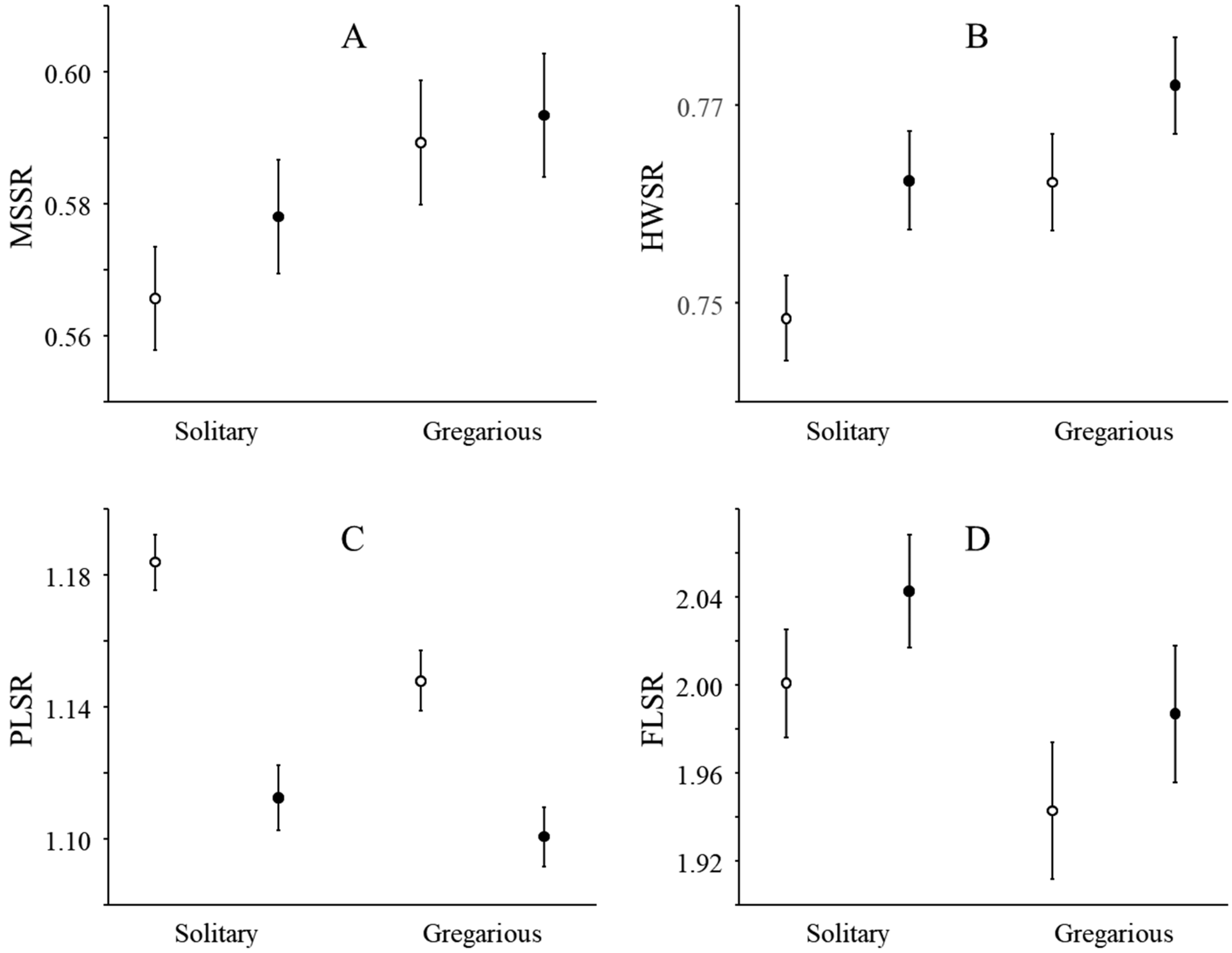

Fig. 3 Shape ratios common to both male (open circles) and female (closed circles) Mormon crickets, *Anabrus simplex*, from both solitary and gregarious populations: (**A**) maxillae span shape ratio (MSSR), (**B**) head width shape ratio (HWSR), (**C**) pronotum length shape ratio (PLSR), and (**D**) femur length shape ratio (FLSR). Bars represent ± 1 SEM. Values are estimated marginal means from the linear mixed models. See text for statistically significant differences

Head width shape ratio

There was no statistically significant effect of the interaction between sex and population type on head width shape ratio ($F_{1,\ 481.96} = 1.061$, $p = 0.303$). After removing the sex by population type interaction, females had larger head width SR than males ($F_{1,\ 477.07} = 44.987$, $p < 0.001$) and gregarious Mormon crickets had larger head width SRs than solitary Mormon crickets, although this difference was not statistically significant ($F_{1,\ 1.64} = 3.841$, $p = 0.093$; Fig. 3B).

Pronotum length shape ratio

Univariate GLMM revealed a significant interaction between sex and population type in their effects on geometric mean size ($F_{1,\ 481.88} = 7.856$, $p = 0.005$). Because of this statistically significant interaction effect [52], we conducted GLMMs for: (1) solitary and gregarious populations separately to test for sexual dimorphism, and (2) males and females separately to test for population differences. Males had larger pronotum length SR than females in both solitary ($F_{1,\ 106.32} = 84.699$, $p < 0.001$) and gregarious ($F_{1,\ 371.42} = 155.350$, $p < 0.001$) populations, and this dimorphism was more pronounced in solitary populations (Fig. 3C). Solitary Mormon crickets had larger pronotum length SR than gregarious Mormon crickets in males ($F_{1,\ 7.08} = 4.837$, $p = 0.063$) but not females ($F_{1,\ 8.93} = 0.600$, $p = 0.459$; Fig. 3C).

Femur length shape ratio

There was no statistically significant effect of the interaction between sex and population type on femur length shape ratio ($F_{1,\ 477.49} = 0.029$, $p = 0.866$). After removing the sex by population type interaction, females had larger femur length SR than males ($F_{1,\ 474.90} = 82.410$, $p < 0.001$) and solitary Mormon crickets had larger femur length SRs than gregarious Mormon crickets, although this difference was not statistically significant ($F_{1,\ 8.16} = 2.106$, $p = 0.184$; Fig. 3D).

Sex-specific genitalic traits

Solitary male Mormon crickets had larger shape ratios than gregarious Mormon crickets for cercus traits, although this difference was not statistically significant for hook length shape ratio (CLSR: $F_{1,\ 7.37} = 17.031$, $p = 0.004$; CWSR: $F_{1,\ 6.96} = 6.718$, $p = 0.036$; HLSR: $F_{1,\ 6.19} = 0.120$, $p = 0.740$; Fig. 4A-C). Solitary female Mormon crickets had larger ovipositor shape ratio than gregarious females, but this difference was not statistically significant ($F_{1,\ 4.58} = 3.487$, $p = 0.126$; Fig. 4D).

Is the Little Brush Creek population more like solitary or gregarious populations?

The discriminant function analysis of male Mormon cricket morphology resulted in a discriminant function that correctly classified 76 of 77 (98.7%) solitary males and 156 of 159 (98.1%) gregarious males ($\chi^2_7 = 362.621$, $p < 0.001$). Head width was the most important morphological trait separating solitary and gregarious males along the discriminant function (Table 3). Cross-validation with individuals from Little Brush Creek (LBC) resulted in all 12 LBC males being classified as gregarious.

The discriminant function analysis of female Mormon cricket morphology resulted in a discriminant function that correctly classified 32 of 33 (97.0%) solitary females and 203 of 217 (93.5%) gregarious females ($\chi^2_5 = 191.848$, $p < 0.001$). Again, head width was the most important

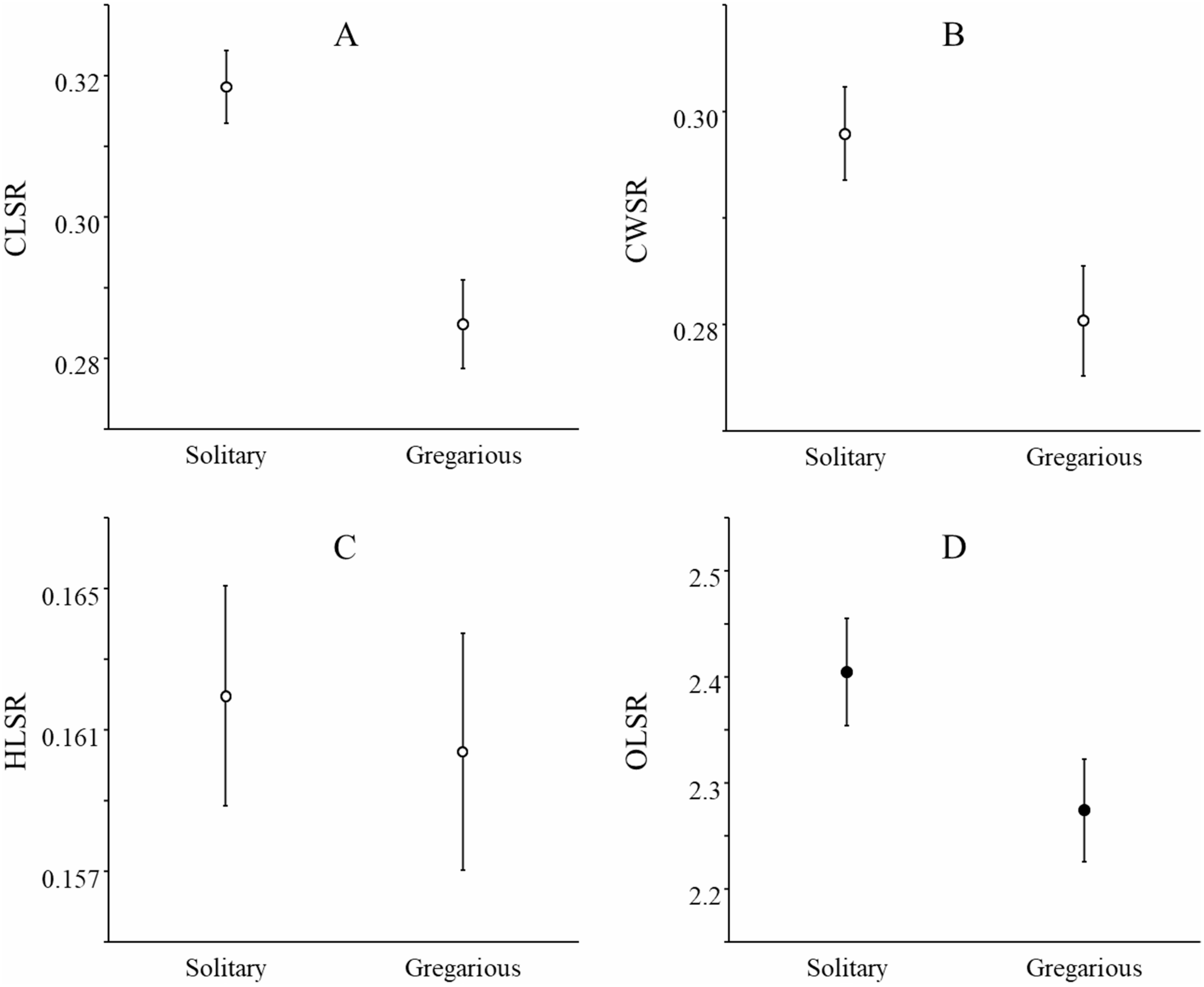

Fig. 4 Shape ratios specific to either male (open circles) or female (closed circles) Mormon crickets, *Anabrus simplex*, from both solitary and gregarious populations: (**A**) cercus length shape ratio (CLSR), (**B**) cercus width shape ratio (CWSR), (**C**) hook length shape ratio (HLSR), and (**D**) ovipositor length shape ratio (OLSR). Bars represent ± 1 SEM. Values are estimated marginal means from the linear mixed models. See text for statistically significant differences

Table 3 Results of three separate discriminant function analyses for male Mormon crickets, *A. simplex*: full (all morphological variables entered simultaneously), Stepwise (backwards), and HW only (only head width entered). The DF (discriminant function) column gives unstandardized function values, and loadings represent correlations between each trait and the DF

	Full		**Stepwise**		**HW Only**	
	DF	**Loadings**	**DF**	**Loadings**	**DF**	**Loadings**
Maxillae Span	-0.179	0.598				
Head Width	3.151	0.930	2.674	0.942	2.604	1.000
Pronotum Length	-0.229	0.559				
Femur Length	-0.062	0.670				
Cercus Length	-2.519	0.239	-2.186	0.242		
Cercus Width	0.885	0.460				
Hook Length	1.608	0.486	1.822	0.492		
Constant	-16.887		-16.988		-20.028	
Eigenvalue	3.822		3.724		3.303	
Canonical Correlation	0.890		0.888		0.876	

Table 4 Results of three separate discriminant function analyses for female Mormon crickets, *A. simplex*: full (all morphological variables entered simultaneously), Stepwise (backwards), and HW only (only head width entered). The DF (discriminant function) column gives unstandardized function values, and loadings represent correlations between each trait and the DF

	Full		**Stepwise**		**HW Only**	
	DF	**Loadings**	**DF**	**Loadings**	**DF**	**Loadings**
Maxillae Span	-0.086	0.554				
Head Width	3.179	0.983	3.059	0.984	2.797	1.000
Pronotum Length	-0.015	0.665				
Femur Length	-0.021	0.636				
Ovipositor Length	-0.132	0.365	-0.139	0.365		
Constant	-22.488		-22.505		-23.803	
Eigenvalue	1.185		1.183		1.145	
Canonical Correlation	0.736		0.736		0.731	

morphological trait separating solitary and gregarious females along the discriminant function (Table 4). As with males, using cross-validation analysis, all 7 LBC females were classified as gregarious.

Distinguishing solitary and gregarious individuals in the field

Setting aside the anomalous LBC population, the above analyses suggested that individuals from solitary and gregarious populations could be distinguished based on a few key measurements. Stepwise discriminant function analyses revealed that head width, cercus length and hook length for males, and head width and ovipositor length for females were the only measurements needed to reliably distinguish solitary and gregarious individuals (Males: $\chi^2_3 = 360.998$, $p < 0.001$; Females: $\chi^2_2 = 192.792$, $p < 0.001$; see Tables 3 and 4 for coefficients; percent correct classifications not shown but similar to above values). However, given that head width is likely the easiest of all our measurements to measure in the field (unlike cerci dimensions) we decided to run discriminant function analyses for each sex using only head width as a predictor variable. The resulting discriminant function for males correctly classified 76 of 77 (98.7%) solitary and 153 of 159 (96.2%) gregarious individuals ($\chi^2_1 = 340.759$, $p < 0.001$; Table 3). The discriminant function for females correctly classified 31 of 33 (93.9%) solitary and 202 of 217 (93.1%) gregarious individuals ($\chi^2_1 = 188.909$, $p < 0.001$; Table 4). The threshold head width for classifying individuals as either solitary or gregarious was 7.43 mm for males and 8.10 mm for females (i.e., solitary < threshold < gregarious, Fig. 5).

Discussion

The primary aim of this paper was to utilize the divergent selection regimes in solitary and gregarious populations of Mormon crickets to test hypotheses derived from both natural and sexual selection, for the evolution of body size and shape. We utilized theory (e.g., [22]) and prior research (e.g., [29]) to formulate a series of predictions about how body size and shape should vary between: (a) solitary and gregarious individuals (population type), and (b) males and females (sexual dimorphism) both within and across population types (Table 1).

Prior work on sexual size dimorphism in Mormon crickets has come to conflicting conclusions about the direction of dimorphism [17,30; see Background for details] that depended on the trait measured (i.e., compare Figs. 1A and B in 30). Using a multivariate measure of size (e.g., [53]), we found that gregarious individuals

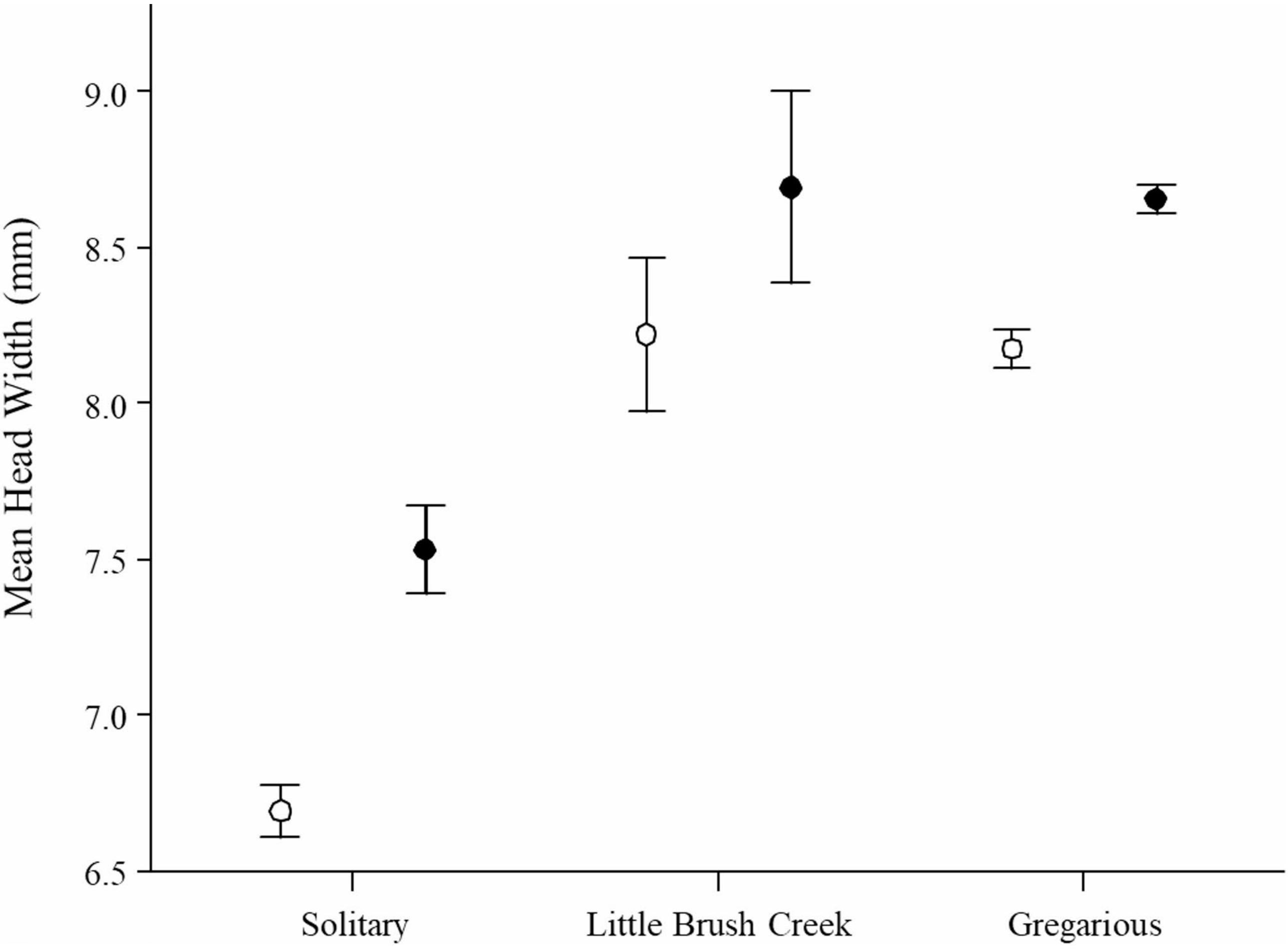

Fig. 5 Mean head width for male (open circles) and female (closed circles) Mormon crickets, *Anabrus simplex*, from solitary and gregarious populations as well as the anomalous population from Little Brush Creek, UT. Bars represent 95% confidence limits

were larger than solitary individuals– consistent with pressures to cannibalize [29]. Moreover, females were larger than males in both solitary and gregarious populations– consistent with both selection for increased fecundity [1, 54] and the general pattern for Orthoptera ([7] but see [53]). However, this sexual size dimorphism was less pronounced in gregarious populations (Fig. 2). This result is consistent with the findings of Bailey et al. [30] and supports our prediction (Table 1) based on Leimar et al.'s [22] verbal model for the development of sexual size dimorphism in nuptial feeding insects. Briefly, in nuptial feeding systems under conditions of food scarcity, females should reduce their investment in body size relative to males, because females stand to lose less than males from small adult body size given females' ability to acquire nutrients from mating [22]. In systems where females are on average larger than males, this results in a reduction of the degree of sexual size dimorphism. Furthermore, reduced female biased sexual size dimorphism in gregarious populations is consistent with sexual selection for smaller females due to scramble competition to locate receptive males quickly (e.g., [40]). Future studies measuring selection on both males and females and both population types would be especially useful in understanding the role that contemporary selection has on shaping sexual dimorphism in body size.

In many animals, males have larger heads than females (e.g., many mammals, [55]; lizards, [56]; wētā, [57]; crickets, [58]; see review by 2 for further examples), and this pattern is thought to be caused by selection for male combat over access to females or resources critical to reproduction (e.g., [56], [34], [59]). In Mormon crickets, we found that females of both population types had relatively wider heads (Fig. 3A) and wider maxillae spans (Fig. 3B) than males. These results are inconsistent with our predictions that sexual selection through intrasexual aggressive competition would favour larger individuals [41] with relatively bigger heads and mouthparts [34] in the sex that competes most for matings (e.g., females in gregarious populations; males in solitary populations [17]). Interestingly, Robson and Gwynne [60] detected direct sexual selection on gregarious females for smaller heads and mandibles. They speculated that their result was indicative of two alternative female strategies for acquiring nutrients: small-headed females that acquire nutrients through matings, and large-headed females that acquire nutrients through cannibalism [60]. They suggest that increased mating rate is a strategy of low condition females and that a selection analysis that used a more direct measure of fitness (e.g., embryos laid) would reveal directional selection for larger heads and mouthparts [60]. Although not statistically significant, we observed relatively larger heads and mouthparts in gregarious populations, suggesting that the pressures of cannibalism have shaped Mormon cricket morphology. That females have relatively larger heads and mouthparts than males supports the importance of these traits to nutrient acquisition given that females are under strong fecundity selection [1, 10]. Pairwise contests over food and/or mates between individuals matched for body size, but with varying head and mouthpart size may provide a fruitful avenue for elucidating the selective pressures on head and mouthpart shape [34].

Gregarious populations of Mormon crickets are rife with cannibalism ([24, 25], DTG and PDL pers. obs.), apparently because individuals are severely protein- and salt-deficient [29]. Pressure to cannibalize conspecifics should select for larger body size and relatively larger feeding and defense structures (head and mouthparts) in gregarious but not solitary populations. Consistent with this, we found that gregarious individuals were larger and had relatively wider heads and maxillae spans, although the head and mouthpart shape differences were not statistically significant. Relatively larger head capsules accommodate larger muscles and thus greater bite force [61]. Similar adaptations for cannibalism are found in amphibian larvae that develop in ephemeral pools of water (e.g., [38]), where rapid growth and metamorphosis to adulthood is essential to escape death due to desiccation when the pool dries up [e.g., 62]. If larger body size and relatively larger head capsules and mouthparts in gregarious Mormon crickets represent adaptation to cannibalism, then there should be a positive relationship between both body size and the SRs of both head width and maxillae span and nutritional status as measured by stable isotope ratios [63].

The combination of an extreme lack of protein and salt with the risk of cannibalism by conspecifics is thought to drive mass migration in gregarious populations [29], in which individuals have been observed to move up to 2 km in a single day [42]. Solitary populations, on the other hand, are stationary. These major differences in locomotory requirements should select for adaptations for increased mobility in gregarious individuals such as: (1) longer femur length SRs for increased relative stride length, and (2) longer pronotum length SRs for increased thoracic muscles used in walking, compared to solitary individuals. In fact, we found the opposite, with solitary individuals having both relatively longer femur length and longer pronotum length, although this latter difference was not statistically significant for females. Instead of adaptation for migration in gregarious populations, increased pronotum length SR in solitary males but not females may be the result of adaptation for increased calling [28], either for amplifying calls [43] or for accommodating increased thoracic musculature for stridulation [64]. Solitary males produce longer, more intense calls with a higher carrier frequency than gregarious males [30], and our findings are consistent with the functional hypothesis that a relatively longer pronotum aids in calling. Also, increased femur length SR– measured on hind legs– in solitary populations may reflect adaptation of these jumping legs to escape predation, whereas individuals in gregarious populations derive protection from predation by being part of a large band [65]. Although we assumed that increased hind femur SR would increase stride length and increase walking efficiency, this is likely dependent on similar changes in pro- and metathoracic legs, which we did not measure. Furthermore, although solitary Mormon crickets had greater hind femur SR, absolute femur length was still shorter than in gregarious Mormon crickets (Supplementary Table 1). Thus, if absolute femur length is more important to mobility than relative femur length, gregarious individuals may still be more mobile than solitary individuals. A more thorough analysis of leg morphology and locomotory ability would be useful in testing our assumptions.

Male Mormon crickets have cerci that grip the female's abdomen during copulation. Our measurements, cercus length and width, reflect the total length of the cerci and thus likely constrain both their maximum gape, and the maximum size of female abdomen a male can grasp. Hook length reflects the length of the medially pointing distal spine on the cercus (Fig. 1), and thus possibly indicates the ability of a male to hold onto a female. Cercus SRs of gregarious and solitary Mormon crickets might simply reflect female body size differences– with larger SRs in the population type displaying greater sexual size dimorphism. Alternatively, however, if male cerci have been subject to different sexual selection pressures in different populations, then hook length SR should be larger in solitary males as an adaptation to enhance male ability to grasp reluctant females (see [66]). We found that solitary males had relatively larger cercus length and width, but not hook length, which suggests that cerci are not adaptations to coerce reluctant females into mating but are simply scaling with the degree of sexual size dimorphism. Comparative analysis has shown an inverse relationship between cercus size and spermatophore size in Tettigoniidae and suggests that these two traits represent equivalent adaptations for securing matings, but with the former being purely coercive [36]. Mormon crickets would be an ideal system in which to test this hypothesis because of the vastly different behaviour of females in gregarious and solitary populations.

The ovipositor of female Mormon crickets extends her body length by approximately 50%, which may incur costs in terms of: (a) decreased mobility, (b) increased difficulty in reaching spermatophylax nuptial meals (females have to curl their abdomens ventrally forward to reach it with their mouthparts), and (c) increased predation risk from visually orienting predators. Alternatively, increased ovipositor length allows females to deposit eggs at: (a) a greater depth to avoid egg predators, and (b) a wider variety of depths to choose optimal oviposition conditions (e.g., temperature). We found that ovipositor length SR was smaller in gregarious females, which is consistent with the fact that mobility and nuptial feeding are important in gregarious populations. This difference may also reflect an adaptation to increase egg-laying depth in higher altitude, possibly wetter locations where solitary populations are found.

Is the Little Brush Creek population more like solitary or gregarious populations?

Our morphological analysis showed that, in size and shape, individuals from LBC were most like gregarious individuals, even though LBC individuals behave like solitary individuals [DTG pers. obs.]. Our findings are consistent with previous genetic work that placed LBC with gregarious populations based on mitochondrial DNA markers [39]. The LBC population is also geographically much closer to gregarious populations than solitary populations [39]. Thus, the LBC population may have come from formerly gregarious individuals that became stationary, first through either temporal (e.g., late adult emergence) or spatial separation and then encountering more abundant food resources. LBC individuals presumably then adjusted their behaviour to that of solitary individuals. This explanation is consistent both with behavioural work showing that individuals from gregarious populations do not march as much when they are isolated from conspecifics [67], as well as the plasticity of Mormon cricket mating roles as shown through experimental manipulation of diet [18].

Distinguishing solitary and gregarious individuals in the field

Finally, discriminant function analyses, done separately by sex, showed head width to be the most important character in classifying specimens correctly into population types. Using these functions, all specimens from Little Brush Creek were classified as being gregarious (Fig. 5). Thus, the discriminant function can be used to assign specimens to population type. In years of low population density, this is likely to be more useful than behaviour for identifying populations of gregarious Mormon crickets that might subsequently become pests in years of high-density.

Conclusions

Our results show that female Mormon crickets are larger than males, and that this difference is more pronounced in solitary populations than in gregarious populations. These findings support previous empirical work by Bailey et al. [30] as well as a theoretical model for the evolution of sexual dimorphism in nuptial gift-giving species [22]. Furthermore, our results for sexual dimorphism in head and mouthpart shape (structures used in aggressive competition for mates, e.g., 34) support predictions (Table 1) stemming from the hypothesis that natural selection, not sexual selection, is the driving force behind sexual dimorphism in Mormon cricket trophic structures. Interestingly, a study of sexual selection on females in gregarious populations– where mating roles are reversed, and females are the competitive sex [17]– found sexual selection for smaller heads and mandibles [60]. Given that females have larger head width and maxillae span SRs than males, this sexual selection pressure may have contributed to the reduction in sexual dimorphism in gregarious relative to solitary populations. To fully elucidate the relative roles of natural and sexual selection in the maintenance of sexual dimorphism, comparisons of selection pressures are needed between gregarious and solitary populations in both females and males. Our results highlight the complex interplay between selective forces in shaping morphology and contribute to a vast and growing literature on the evolution of sexual dimorphism [68].

All populations of *A. simplex* studied so far have been categorized into two distinct groups– solitary and gregarious– based on their behaviour (see Background for detailed description). However, genetic, morphological, and acoustic studies have revealed one enigmatic population: behaviourally solitary, but more like gregarious populations in every other way measured [30, 39, this study]. We found that it was possible to classify correctly over 93% of individuals into solitary or gregarious phases based solely on a single morphological dimension, head width. This result, when combined with the selection analysis results on head width [60], suggests that further research on the relative importance of diet, cannibalism and intrasexual competition would be worthwhile.

Supplementary Information

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Supplementary Material 1

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Author contributions
KAJ conceived of the study, organized data collection, analyzed the data and drafted the manuscript. SRD and LJR performed statistical analyses and helped to draft the manuscript, LJR also collected some of the measurements. PDL collected specimens and drafted the manuscript. CJV advised on statistical analysis and interpretation of shape ratios. DTG collected specimens and helped to draft the manuscript. All authors read, edited, and approved the final manuscript.

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Data availability
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request, and will be made publicly available on Dryad in advance of final publication.

Declarations

Ethics approval and consent to participate
The collection of specimens complied with all national and institutional guidelines. No collection permits were required for this study.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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