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Research Article

The quantitative genetic basis of female and male body size and their implications on the evolution of body size dimorphism in the house cricket *Acheta domesticus* (Gryllidae)

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Abstract

Few theoretical and experimental studies have analyzed the genetic basis of body size dimorphism. Since the evolutionary response to selection depends of the genetic variance in a population it is to be expected that traits under selection would have smaller genetic variance than traits not affected by selection. The evolution of sexual size dimorphism is affected by the genetic correlation between females and males, with the most dimorphic traits showing smaller genetic correlations between the sexes. As result of the differences in the intensity of sexual selection between the sexes, it is expected that the levels of genetic variance would be larger in females than males. I analyzed the genetic additive variance underlying six traits of *Acheta domesticus*, and the genetic correlations between females and males. The most dimorphic trait with the smallest genetic correlation between the sexes was forewing length, this trait showing genetic variance only in females. It may be that sexual selection acting on male traits has depleted the genetic variance not only in male traits but also for those female traits that have a large genetic correlation with male traits. It is also possible that the evolution of sexual dimorphism in *A. domesticus* could be constrained as a result of the large genetic correlation between the sexes.

Key words: Acheta domesticus, body size, dimorphism, heritability, sexual selection.

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Introduction

Phenotypic differences between sexes can arise as result of sexual differences in the intensity or mode of selection (Badyaev *et al*., 2000; Krausaar and Blanckernhorn, 2002). Falconer (1989) has pointed out that the evolutionary response to selection depends on the quantitative genetic variance in the population and that the amount of genetic variance present in a population can reflect the historical consequences of natural selection, because of which it is to be expected that genetic variance would be depleted by natural selection.

Since sexual selection is generally stronger on males than females (Andersson, 1994), it is to be expected that the levels of genetic variance underlying sexually-selected traits would be larger in females than males because of the differences in the intensity of sexual selection between the sexes. However, the genetic variance of traits undergoing natural selection can be affected by several genetic factors, including the relationship of each trait to fitness (Falconer 1989), genetic correlation between characters (Stearns, 1992; Roff, 1996; Houle, 2001) and the effect of the environment on the traits, including whether the traits are condition-dependent (Rowe and Houle, 1996; Schlichting and Pigliucci, 1998; Nager *et al.*, 2000, Tomkins *et al*., 2004).

When calculating the effects of traits that show sexual dimorphism it is necessary to consider genetic correlations between sexes (Lande, 1980). If the correlation between the sexes is large there are two alternative scenarios; the genetic variance in females can decrease in a correlated response to selection pressure on males, or, if natural selection is operating in a different way on females than on males, it is possible that the genetic variance will be maintained in the population due to an equilibrium between female and male selective pressures (Simmons and Ward, 1991). Despite these evolutionary implications, only a few experimental studies have analyzed the genetic basis of body size dimorphism (Simmons and Ward, 1991; Reeve and Fairbairn, 1996; Merila *et al*., 1998; Badyaev and Hill, 2000).

The study presented in this paper analyzes the genetic variance of six traits of female and male *Acheta domesticus* (house crickets). Female house crickets prefer the song patterns of large males, which, consequently, have higher mating success (Gray, 1997). As a consequence of this sexual

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selection I hypothesized that non-dimorphic traits should show less genetic variance than dimorphic traits (Rowe and Houle, 1996), for which males are expected to show less genetic variance than females. Differences between the genetic variance of dimorphic traits should be related to the genetic correlation between sexes, with female traits that are more closely correlated with male traits exhibiting less genetic variance than traits with lower genetic correlations.

Material and Methods

Cricket stocks

A half-sib cross-breeding design was performed to estimate the heritability of six morphological traits of the house cricket *Acheta domesticus* (Gryllidae), from a four year old laboratory stock held at the university of Toronto. This stock having originally been derived from about 200 house crickets obtained from a local pet supply store. In this experiment each male was crossed with two females by placing a male and a female together in a 500 ml plastic container for three days, after which the first female was replaced with another which was also left with the male for three days. After exposure to the male, the females were transferred to individual containers with vermiculite until their eggs hatched, the offspring being transferred to one-litre housing jars until they reached sexual maturity. In all cases food (cricket chow; Fluker Farms) and water were provided *ad libitum* each third day. When the offspring were close to sexual maturity the rearing jars were checked daily for newly molted adults, which were removed from the jars, sacrificed and individually preserved in 70% (w/v) aqueous ethanol. At the end of the experiment, digital pictures of the experimental progenies were taken with a video camera (Hitachi; VK-C370) and an image analyzer (Windias 1.5 Delta-T Devices Ltd.) used to measure the following parameters for each sex: pronotum length and width, left and right hind tibia length, and left and right forewing length.

Statistical analysis

Body size dimorphism

Multivariate analysis of variance (MANOVA) was performed to test for body size dimorphism of the six female and male morphological traits, *t*-tests being conducted to detect which of the six measured traits were sexually dimorphic. The coefficient of variation (CV) were also estimated for each trait.

Genetic correlation

The family mean values of each sex were estimated for the dimorphic traits, and Pearson correlations performed between sexes for each trait. Because the family mean method may be biased when family size is small ($\approx < 20$) the confidence intervals for the correlations were estimated using a jackknife procedure (Roff and Preziosi, 1994). Monte Carlo simulations were used to obtain the confidence intervals of the significant correlation coefficients.

Heritability

For traits showing sexual dimorphism, heritability was calculated for each sex. In non-dimorphic traits the heritability obtained was a combined female+male heritability estimation. For each trait nested ANOVAs (Model II, Type III SS, Sokal and Rohlf, 1995) using the GLM module of the JMP procedure (SAS, 1995) were performed to determine the presence of a significant sire effect. Genetic variance components which differed from zero were tested using the SAS Proc Mixed module (SAS, 1999), this analysis showing whether or not a given additive genetic variance estimate is different from zero. Heritability was estimated as the ratio of the sire component of variance to the total phenotypic variance.

Results

Sexual size dimorphism

The analysis indicated that morphological differences existed between the sexes (MANOVA Wilks's $\lambda = 0.922$; $F_{(6;\,257)} = 3.566$; $p < 0.001$). Left and right hind tibia length, left and right forewing length, and pronotum width all showed sexual dimorphism. These traits were larger in females than males, while thorax length did not differ between sexes (Table 1). Moreover, females showed more variation than males as regards forewings and the pronotum (Table 2).

Table 1 - Mean plus standard error (SE) of the six morphological traits in female and male of *Acheta domesticus* crickets. The *P* values are from two-tailed *t* test (262 degrees of freedom) of differences between sexes.

Trait (mm)	Females	Males	*t*	p
Left hind tibia length	9.086 (0.063)	8.757(0.059)	3.794	< 0.0001
Right hind tibia length	9.097 (0.059)	8.852 (0.064)	2.794	0.0005
Left forewing length	10.346 (0.083)	10.062 (0.077)	2.510	0.013
Right forewing length	10.363 (0.083)	10.095 (0.077)	2.361	0.019
Pronotum length	2.941 (0.033)	2.940 (0.031)	0.011	0.990
Pronotum width	4.219 (0.038)	4.103 (0.038)	2.193	0.029

Table 2 - Coefficients of variation (CV) of the six morphological traits measured in female and male *Acheta domesticus* crickets.

Sex	Hind tibia		Forewing		Pronotum	Pronotum
	Left	Right	Left	Right		
Females	11.46	10.22	8.71	8.50	9.69	9.65
Males	13.72	10.80	7.68	7.84	8.41	8.41

Genetic correlations

High genetic correlations were found between all the measured traits (Table 3a-c). Genetic correlations between the sexes were significant and varied from 0.888 between the female left hind tibia length and the male right hind tibia length to 0.661 between male pronotum width and female right forewing. The lowest genetic correlations were found between female and male forewing length and all traits of the opposite sex (Table 3c). The genetic correlations remain significant after Monte Carlo simulations.

Heritability

Female traits showed significant levels of sire variation (Table 4a). However, only their forewing lengths showed significant heritability. Left and right female hind tibia length were marginally non-significant (h^2 = 0.427; p = 0.064; h^2 = 0.398; p = 0.061; respectively), as were the maternal effects (Dam Sire) on female left, and male left and right tibias (Table 5).

Discussion

The results showed that tibia length, forewing length and pronotum width are sexually dimorphic in *A. domesticus*. Females were larger than males in all three measures, and there were differences between sexes in the genetic correlations. The smaller correlations were found between female forewing lengths with all the male traits (Table 3c). Interestingly, in four of the six traits females

Table 3a - Genetic correlations between the six morphological traits of *Acheta domesticus* females (n = 123). Jackknife significance levels are shown between parenthesis.

	Right hind tibia length	Left forewing length	Right forewing length	Pronotum width	Pronotum length
Left hind tibia length	0.995 (< 0.001)	0.914 (< 0.001)	0.900 (< 0.001)	0.954 (< 0.001)	0.728 (< 0.017)
Right hind tibia length		0.904 (< 0.001)	0.900 (< 0.001)	0.954 (< 0.001)	0.757 (0.011)
Left forewing length			0.996 (0.001)	0.933 (< 0.001)	0.670 (0.033)
Right forewing length				0.933 (< 0.001)	0.696 (0.025)
Pronotum width					0.803 (0.005)

Table 3b - Genetic correlations between the six morphological traits of *Acheta domesticus* males (n = 141). Jackknife significance levels are shown between parenthesis.

	Right hind tibia length	Left forewing length	Right forewing length	Pronotum width	Pronotum length
Left hind tibia length	0.955 (< 0.001)	0.722 (0.018)	0.728 (0.016)	0.883 (< 0.001)	0.923 (< 0.001)
Right hind tibia length		0.781 (0.007)	0.770 (0.009)	0.955 (< 0.001)	0.924 (< 0.001)
Left forewing length			0.781 (0.007)	0.796 (0.006)	0.706 (0.022)
Right forewing length				0.783 (0.007)	0.687 (0.028)
Pronotum width					0.888 (< 0.001)

Table 3c - Genetic correlations between female and male (n = 264) dimorphic traits of *Acheta domesticus*. Jackknife significance levels are shown between parentheses.

	Male trait				
Female Trait	Left hind tibia length	Right hind tibia length	Left forewing length	Right forewing length	Pronotum width
Pronotum width	0.865 (< 0.001)	0.881 (< 0.001)	0.843 (0.006)	0.848 (0.005)	0.810 (0.001)
Left hind tibia length	0.856 (< 0.001)	0.888 (< 0.001)	0.746 (0.003)	0.730 (0.004)	0.780 (< 0.001)
Right hind tibia length	0.867 (0.001)	0.887 (0.001)	0.730 (0.002)	0.719 (0.002)	0.788 (< 0.001)
Left forewing length	0.704 (< 0.001)	0.725 (< 0.001)	0.788 (< 0.001)	0.792 (< 0.001)	0.696 (< 0.001)
Right forewing length	0.710 (0.002)	0.742 (0.002)	0.797 (< 0.001)	0.799 (< 0.001)	0.661 (< 0.001)

Table 4a - ANOVA of five dimorphic traits of *Acheta domesticus*. Sire and dams nested in sire (Dam [Sire]) were considered random effects.

Left hind tibia length										
		Females					Males			
Source	SS	df	F	p	r^2	SS	df	*F*	p	r^2
Sire	27.222	9	3.406	0.033	0.427	18.056	9	1.764	0.192	0.274
Dam [Sire]	9.125	10	3.400	< 0.001	0.143	11.8755	10	4.327	< 0.001	0.180
Error	27.638	121				33.202	121			
Right hind tibia length										
		Females					Males			
Source	SS	df	*F*	p	r^2	SS	df	*F*	p	r^2
Sire	25.150	9	3.464	0.031	0.370	18.484	9	2.182	0.117	0.288
Dam [Sire]	8.250	10	2.422	0.012	0.121	9.806	10	3.718	< 0.001	0.153
Error	67.832	121				64.077	121			
Left forewing length										
		Females					Males			
Source	SS	df	*F*	p	r^2	SS	df	*F*	p	r^2
Sire	39.682	9	3.737	0.024	0.326	35.819	9	2.629	0.071	0.358
Dam [Sire]	12.038	10	2.126	0.028	0.099	15.778	10	3.740	0.001	0.158
Error	58.324	121				51.040	121			
Right forewing length										
		Females					Males			
Source	SS	df	*F*	p	r^2	SS	df	*F*	p	r^2
Sire	36.374	9	3.421	0.032	0.301	32.299	9	2.542	0.078	0.315
Dam [Sire]	12.052	10	2.089	0.031	0.099	14.666	10	3.105	0.001	0.143
Error	59.424	121				57.144	121			
Pronotum width										
		Females					Males			
Source	SS	df	*F*	p	r^2	SS	df	*F*	p	r^2
Sire	4.864	9	2.341	0.098	0.234	6.146	9	2.012	0.141	0.005
Dam [Sire]	2.356	10	2.160	0.026	0.113	3.518	10	2.773	0.004	0.229
Error	20.734	121				15.350	121			

Key: SS = Sum of Square; *df* = degrees of freedom; *F* = F-value; p = probability level; r^2 = explained variance.

Table 4b - ANOVA of a not dimorphic trait; pronotum length of *Acheta domesticus.* Sire and Dam nested in Sire (Dam [Sire]) was considered random effect.

Source	SS	df	*F*	p	r^2
Sire	6.787	9	2.667	0.055	0.190
Dam [Sire]	3.489	11	3.026	0.0008	0.097
Error	25.475	263			

Key: SS = Sum of Square; *df* = degrees of freedom; *F* = F-value; p = probability level; r^2 = explained variance.

showed more variation than males (Table 2). Nevertheless, only female forewing length showed significant heritability. These results are consistent with my predictions. In general, sexual selection is stronger on males than females (Andersson, 1994). As a result of female choice, the genetic variance in male traits that are preferred by females and female traits strongly genetically correlated with them (see Tables 4b and 5b), could have been eroded by sexual selec-

Table 5a - Variance components estimates and heritabilities (h^2) of five dimorphic traits *of Acheta domesticus* ($n_{females} = 123$; $n_{males} = 141$). Sire and Dams nested in Sire were considered random effects. *P*-values were obtained from a *Z*-test (variance component divided by standard error (SE)).

	Left hind tibia length									
	Females					Males				
Source	Estimate	SE	Z	h^2	p	Estimate	SE	Z	h^2	p
Sire	0.340	0.224	1.52	0.427	0.064	0.151	0.130	1.16	0.270	0.123
Dam [Sire]	0.166	0.105	1.35		0.057	0.141	0.094	1.52		0.063
Residual	0.291	0.040	7.16		< 0.001	0.266	0.034	7.72		< 0.001
	Right hind tibia length									
	Females					Males				
Source	Estimate	SE	Z	h^2	p	Estimate	SE	Z	h^2	p
Sire	0.318	0.206	1.54	0.398	0.061	0.155	0.134	1.16	0.275	0.123
Dam [Sire]	0.116	0.086	1.35		0.088	0.141	0.093	1.52		0.063
Residual	0.364	0.051	7.16		< 0.001	0.266	0.035	7.72		< 0.001
	Left forewing length									
	Females					Males				
Source	Estimate	SE	Z	h^2	p	Estimate	SE	Z	h^2	p
Sire	0.469	0.283	1.66	0.412	0.048	0.087	0.123	0.71	0.154	0.239
Dam [Sire]	0.089	0.076	1.18		0.119	0.199	0.123	1.61		0.053
Residual	0.579	0.079	7.32		< 0.001	0.278	0.036	7.70		< 0.001
	Right forewing length									
	Females					Males				
Source	Estimate	SE	Z	h^2	p	Estimate	SE	Z	h^2	p
Sire	0.432	0.262	1.64	0.388	0.050	0.200	0.162	1.24	0.241	0.107
Dam [Sire]	0.086	0.076	1.12		0.132	0.151	0.114	1.32		0.093
Residual	0.593	0.081	7.33		< 0.001	0.478	0.062	7.71		< 0.001
	Pronotum width									
	Females					Males				
Source	Estimate	SE	Z	h^2	p	Estimate	SE	Z	h^2	p
Sire	0.062	0.046	1.32	0.296	0.093	0.061	0.053	1.15	0.260	0.124
Dam [Sire]	0.034	0.024	1.46		0.081	0.046	0.035	1.33		0.092
Residual	0.113	0.015	7.24		< 0.001	0.127	0.016	7.72		< 0.001

tion. The smallest genetic correlation between female forewing length and male characters can explain why the forewing was the most dimorphic trait and showed significant genetic variance levels. When the genetic correlations between the sexes are small the independent evolution of male and females is possible and sexual dimorphism can evolve (Lande, 1980; Lynch and Walsh, 1998).

If the genetic variance in male traits under sexual selection is small the possibility that an evolutionary response to selection occurs would be reduced and environmental factors like diet, or temperature can strongly affect the phenotypes (Moreteau *et al.*, 1994; Nager *et al.*, 2000; Thompson, 1999). In this study body size traits variation appear not to be reliable indicators of male genetic quality but can suggest the condition of the male to a potential mate. Nevertheless, Bakker and Pomiankowski (1995) found high genetic variance in male traits under sexual selection. Rowe and Houle (1996) consider that sexually selected traits maintain genetic variation because they are influenced by a large number of loci, which results in a relatively high frequency of mutations in genes coding for their phenotypic expression. However, other alternative hypotheses are possible. If genetic correlation between the sexes is high, and natural and/or sexual selection are operating in different ways on each sex, the genetic variance would be maintained in the population as result of a tradeoff (Simmons and Ward, 1991). Also, if the genetic correlation between the sexes is small, and females traits are not the

Table 5b - Mixed variance model for heritability (h^2) of a non-dimorphic trait (pronotum length) of *Acheta domesticus* (n = 264). Sire and Dam nested in Sire (Dam Sire) was considered random effect.

Source	Estimate	SE	Z	h^2	p
Sire	0.028	0.023	1.26	0.183	0.103
Dam [Sire]	0.020	0.014	1.44		0.075
Residual	0.105	0.009	10.99		< 0.001

Key: SE = Standard Error; *Z* = Z-value p = probability level.

target of selection, some level of genetic variance could be restored to next generation males as result of sexual recombination.

Sexually selected traits are homologous characters, so the analysis of inter-sexual genetic variance and genetic correlations between sexes can assist understanding the evolution of sexual dimorphism and the effects of sexual and natural selection in the levels of genetic variance within sexes.

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