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Author(s): Ketola, Tarmo; Kortet, Raine; Kotiaho, Janne Sakari

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Testing theories of sexual selection in decorated crickets (*Gryllodes sigillatus*)

Tarmo Ketola,[1]* Raine Kortet[1,3] and Janne S. Kotiaho[1,2]

[1]*Department of Biological and Environmental Science and* [2]*Natural History Museum, University of Jyväskylä, Jyväskylä and* [3]*Section of Ecology, Department of Biology, University of Oulu, Oulu, Finland*

ABSTRACT

Question: Do females choose males according to their level of acoustic sexual activity, fluctuating asymmetry, size, condition or do they select for genetic compatibility according to relatedness? What are the relative strengths of selection on these traits and what might be the benefit of the choice – large nuptial gifts, heritable attractiveness or quality?

Organism: Laboratory colony of decorated crickets (*Gryllodes sigillatus*).

Methods: Behavioural trial of female preference on male traits, multivariate logistic regression of male traits on female preference, and heritability estimation of the traits with an animal model.

Results: Female attraction strongly discriminated in favour of certain male courtship call rates. None of the other potential cues, such as size-dependent traits, fluctuating asymmetry or relatedness were involved in sexual selection. In addition, no evidence of benefits of the attraction was found. However, if the cost of choice for females is low, then the potential genetic benefits outweighing it might be smaller than what can be estimated with this data set. Moreover, the signal itself is a strong species-specific signal that facilitates mate location and helps to prevent maladaptive hybridization. Thus, the signal itself may be considered a benefit without any additional correlated benefits.

Keywords: attraction, direct benefits, genetic compatibility, indirect benefits, pre-mating sexual selection.

INTRODUCTION

Sexual selection through female choice suggests that females prefer males with elaborate sexual signals as mates because they can gain direct or indirect, heritable, benefits from mating with such males (e.g. Andersson, 1994; Andersson and Iwasa, 1996; Kokko *et al.*, 2003; Andersson and Simmons, 2006). A prerequisite for a trait to have potential to indicate benefits is that the trait is related to the benefit. On the other hand, any benefits the trait might indicate cannot be realized if male mating success is not biased in relation to the trait. By examining these

* Author to whom all correspondence should be addressed. e-mail: tketola@jyu.fi
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relations and features, we can determine whether the trait has the potential to be used as an indicator trait and whether this potential could be realized via pre-mating sexual selection.

Indirect, additive genetic benefits may be obtained through increased mating success of sexy sons or through the increased fitness of offspring inheriting good genes (e.g. Lande, 1981; Kirkpatrick and Barton, 1997). For indirect genetic benefits to be realized in an indicator trait, it must be heritable. In the good genes hypothesis, a positive genetic correlation between the surrogate of the good genes and the indicator trait is also needed (Andersson, 1994; Alatalo *et al.*, 1997; Kotiaho *et al.*, 2001). Often, a large indicator trait is expected to convey information about male quality, since only high-quality males can bear the cost associated with an elaborate sexual signal (e.g. Andersson, 1982, 1986). Another suggested avenue for the good genes type of indirect genetic benefit is through assessing the symmetry of the traits. An individual's ability to withstand genetic and environmental stress during development may be expected to result in perfectly symmetrical bilateral traits; random deviations from perfect symmetry (i.e. fluctuating asymmetry) should indicate poor genetic quality (Watson and Thornhill, 1994; Møller, 1997; Møller and Swaddle, 1997; Simmons *et al.*, 1999; Tomkins and Kotiaho, 2001). In crickets, it has been suggested that information about male quality is acquired via acoustic signalling; the quality of the signal may indeed be reflected through the symmetry of the primary sound radiators (Simmons and Ritchie, 1996).

Sexual selection based on sexy sons or good genes, or in fact any mechanism based on additive genetic benefits, assumes that a particular male that is a good choice for one female is a good choice for every female. However, indirect genetic benefits to females may also be based on genetic compatibility of male and female genotypes (Tregenza and Wedell, 2000; Colegrave *et al.*, 2002; Mays and Hill, 2004; Neff and Pitcher, 2005). Intra-genomic conflict, such as selfish genetic elements (Zeh and Zeh, 1996), heterozygote advantage, avoidance of deleterious mutations or avoidance of a co-adapted gene complex breakage may drive female choice for genetic compatibility (Tregenza and Wedell, 2000; Puurtinen *et al.*, 2005). Recognition of compatible partners is suggested to be possible by using information on similarity, as in the case of MHC-alleles (Roberts and Gossling, 2003). In insects, there is some evidence that compatibility information may be acquired from cuticular hydrocarbons functioning as pheromones (e.g. Simmons, 1989; Tregenza and Wedell, 1997).

Acquiring indirect genetic benefits by pre-copulatory choice is strictly determined by the genetic architecture of the trait: additive genetic variation may drive the choice for good genes, while epistatic and dominance variation dictate compatibility choice. However, direct benefits are always possible if they are correlated with the indicator trait or signal. Moreover, the signal itself may be considered a benefit without any additional benefits: strong species-specific signals may benefit the females in terms of easing the mate location (Kirkpatrick and Ryan, 1991; Alatalo *et al.*, 1998; Hack, 1998; Kokko and Mappes, 2005) and preventing maladaptive hybridization (Dobzhansky, 1951; Sætre *et al.*, 1997; Tynkkynen *et al.*, 2005, 2006).

Theories of sexual selection are often tested separately and choosing for compatibility is rarely even considered. In crickets in particular, the emphasis has been strongly biased towards acoustic signals (e.g. Hedrick, 1986; Gray and Cade, 1999; Wagner and Reiser, 2000). In fact, even studies that concentrate on indirect and direct benefits simultaneously via pre-copulatory choice are scarce (Widemo and Saether, 1999; Kokko *et al.*, 2003; Neff and Pitcher, 2005). Although it might be fashionable (under the current paradigm) and more practical to test only one theory at a time, it nevertheless prevents estimation of the relative importance of different components of mate choice and hence hinders obtaining a more general picture of sexual selection.

Our aim in this study was to build a comprehensive picture of sexual selection through mate choice in the decorated cricket *Gryllodes sigillatus* (Orthoptera: Gryllidae). To do this, we estimated the magnitude of sexual selection on courtship call rate, various morphological traits, and on genetic compatibility. In addition, we determined whether the trait that had an effect on male mating success fulfilled the prerequisites for being an indicator of potential benefits. We tested the potential for direct benefits by relating the trait with the size of the nuptial gifts. The potential for indirect benefits was examined by estimating the additive genetic variance and heritability of the trait, and by determining the genetic correlation between the trait and surrogates of genetic quality such as physical condition and longevity.

METHODS

Pair formation of the decorated cricket includes acoustic signals, which are produced by a resonating harp, a thickened membrane on each wing that functions as a primary sound radiator. Male crickets produce two types of acoustic signals: a long-range calling song used to attract females from a distance, and a courtship song used just before mating (Sakaluk, 1987; Loher and Dambach, 1989). These acoustic signals might inform females about potential benefits males provide. For example, sound quality may be affected by fluctuating asymmetry (Simmons and Ritchie, 1996) and the calling is energetically demanding (e.g. Hack, 1998). Therefore, calling might mediate information about heritable male quality. In addition, pheromones are involved in pair formation in some cricket species, including *Gryllus bimaculatus* (Simmons, 1989; Tregenza and Wedell, 1997), *Gryllus integer* (Kortet and Hedrick, 2005), and *Gryllodes sigillatus* (Ivy *et al.*, 2005), hence providing a possibility for females to accrue information about relatedness (Simmons, 1989) and genetic compatibility of the males. *Gryllodes sigillatus* males produce spermatophores with large gelatinous spermatophylax, which may act as a nuptial gift and hence provide direct benefits (e.g. Ivy *et al.*, 1999).

Study population and structure of the pedigree

Gryllodes sigillatus individuals for this study were obtained from a population that was kept in our laboratory at the University of Jyväskylä, Finland for six generations prior to the experiment. The first generation was initiated from eggs of 48 females that were wild caught from a large, and hence likely outbred, population at the campus of the University of Western Australia. Families have been kept at a 12 h : 12 h photoperiod at 30°C with a relative humidity of 58%. They were provided with food (dried cat and rabbit food) and water *ad libitum*. A pedigree of all individuals was maintained from the initiation of the laboratory population. Each generation was initiated by pairing several males from each family to females from different families to form 50–150 families. Throughout all generations, close inbreeding was avoided. The final pedigree used for the analysis consisted of descendants of 25 wild-caught females (~52% of the initial starting population). In the analysis, we considered the first-generation families to have different and unrelated fathers. Altogether our pedigree totalled approximately 500 individuals. The sixth-generation individuals measured were from about 30 families (Table 1). In addition to this within-family relatedness, the individuals were more distantly related with members of some other families. Coefficients of co-ancestries between individuals within families varied between 0.25 and 0.3, whereas variation between individuals belonging to different families was

Table 1. Descriptive statistics, heritabilities (h^2), and coefficients of additive genetic variation (CV_A) of measured traits

Trait	Families	n	Mean	Phenotypic variance	h^2 (standard error)	CV_A
Courtship call rate (frequency)	25	110	0.3047	0.0788	0.249 (0.188) $P = 0.089$	46.18
Harp size (mm^2)	25	96	0.0694	0.570×10^{-4}	0.541 (0.243) $P = 0.013$	8.09
FA harp (mm^2)	25	96	0.00253	0.259×10^{-5}	0 (0)	—
FA global (PC1)	25	86	0.0309	0.890	0.341 (0.245) $P = 0.082$	1804.77
Weight (mg)	24	121	252.6	1978.4	0.402 (0.199) $P = 0.018$	11.27
Condition (RBM)	24	100	252.7	558.2	0.350 (0.194) $P = 0.035$	5.08
Size (PC1)	24	102	0.014	1.042	0.548 (0.238) $P = 0.011$	5416.34
Relatedness ($\theta_{m,f}$)	25	124	0.0496	0.001	—	—
Longevity (days)	30	138	46.72	658.8	0.517 (0.201) $P = 0.005$	39.62
Longevity, males (days)	30	55	48.95	578.6	0.643 (0.376) $P = 0.044$	39.52
Longevity, females (days)	30	83	45.42	715.2	0.386 (0.245) $P = 0.057$	36.52

Note: CV_A was not obtainable from the harp. See 'Materials and methods' for explanation of spuriously high CV_A in principal components. The significances of heritabilities were obtained by one-way tests with the *a priori* expectation that heritabilities are greater than zero. FA = fluctuating asymmetry, RBM = residual body mass.

either 0 or varied between 0.025 and 0.075. Individuals for the study were collected from the F_6-generation and they were reared individually from very early developmental stages in one-litre plastic containers with food and water *ad libitum*. This was done to exclude as far as possible any common environmental effects and to control for experience as well as virginity of the individuals.

Data analysis was performed mainly using SPSS v.12.0 (SPSS Inc., Chicago, IL, USA). However, genotypic and phenotypic variances and co-variances for traits were extracted using an animal model and restricted maximum likelihood methods in ASReml 1.10 software (VSN International Ltd., Hemel Hempstead, UK). Throughout this paper we only consider male traits. The only exception is longevity, where also female values are reported. The longevity of individuals was measured from individuals that were related to the assessed individuals. These individuals were reared in conditions similar to those of assessed individuals until death. Longevity was calculated as a time, in days, from maturation to death.

Courtship behaviour

Courtship behaviour trials were performed on crickets at the age of 7 days (±1 day) after the final moult to ensure maturation, at a mean temperature of 30°C (±2°C) with dim red

lighting. The trial arena was a 25 × 25 × 20 cm plastic container with 5 cm of vermiculite on the bottom. Trials were initiated by placing a weighed male and female in their own small containers inside the arena. After 5 min acclimation, the small containers were carefully removed. For each trial, we monitored courtship call rate for the first 2 min or until mating occurred if it was before the 2 min had elapsed. Courtship call rate was obtained by observing the male calling (call, not call) every 10 s. We did not consider male long-distance calling since it is actually the courtship song that proximately precedes the female's decision to mate with a male. In *G. sigillatus*, a female mounts on top of a male when she is ready to mate. Therefore, it is likely that there is no opportunity for males to force copulation. We chose this definite measure of male mating success, because a female's decision to mount a male potentially also includes pheromones or cuticular hydrocarbons. These types of chemical cues might play a role in kin recognition or provide information on the male's social status [e.g. in *G. bimaculatus* (Simmons, 1989; Tregenza and Wedell, 1997) and *G. integer* (Kortet and Hedrick, 2005)]. Each trial lasted up to 20 min. In total, we performed 126 trials, of which 50 ended on mating.

Immediately after mating, the female was placed on dry ice to prevent consumption of spermatophylax and transfer of sperm from ampulla. The collected ampulla ($n = 45$) and spermathophylax ($n = 35$) of the spermatophore were weighed. We were able to obtain sperm traits only from those males that females mated with and hence neither ampulla nor spermatophylax weight was included in the selection analyses. As the sample size of these traits was relatively small, we excluded them also from the genetic analyses. Thus, these traits were only compared phenotypically to other traits to determine whether females might gain direct benefits from mating with particular males. Due to the pedigree spanning over six generations, we were able to calculate the coefficient of co-ancestry between the male and female [$\theta_{\mathbf{m,f}}$ (Lynch and Walsh, 1998)] and determine whether relatedness, indicated by this coefficient, was under selection due to choice for compatibility.

Morphological measurements

Morphological traits that we measured were tibia length, pronotum width, size of the forewings, and size of the harp. Tibia length and pronotum width were measured with a binocular microscope with eyepiece graticule. To assess repeatability of the measurements, every individual was measured twice on separate occasions and repeatability was calculated according to Lessells and Boag (1987); all measurements were highly repeatable [pronotum width: $r = 0.991$, $F_{113,105} = 21.48$, $P < 0.001$; tibia length (right): $r = 0.826$, $F_{107,98} = 10.47$, $P < 0.001$; tibia length (left): $r = 0.888$, $F_{109,101} = 16.85$, $P < 0.001$]. Wing morphology was measured from photographs of the wings that were taken using a binocular microscope attached to a video camera. Areas of the wings and the harps were measured from digitized images using Image-Pro v. 4.5 (Media Cybernetics, Silver Spring, MD, USA). To assess repeatability of this method, we performed a separate test with 20 pairs of wings and repeated the whole measurement protocol twice. We found that the difference between the two computer-assisted measurements was practically non-existent [wing size (right): $r = 0.998$, $F_{40,41} = 1226.79$, $P < 0.001$; wing size (left): $r = 0.991$, $F_{40,41} = 220.64$, $P < 0.001$; harp size (right): $r = 0.968$, $F_{37,38} = 61.73$, $P < 0.001$; harp size (left): $r = 0.993$, $F_{38,39} = 28.88$, $P < 0.001$).

From morphological measurements, we calculated fluctuating asymmetry, which is the unsigned difference of left and right sides of a structure (e.g. wings). We did not observe

directional asymmetry (signed fluctuating asymmetry) in any of the measurements – that is, deviation from the mean of zero (tibia: $t_{95} = -0.523$, $P = 0.602$; wing: $t_{93} = 0.012$, $P = 0.990$; harp: $t_{97} = -0.123$, $P = 0.902$). Fluctuating asymmetry was not related to trait size (tibia: $\beta_{95} = 0.023$, $P = 0.213$; wing: $\beta_{93} = -0.029$, $P = 0.163$; harp: $\beta_{97} = -0.01$, $P = 0.924$).

Altogether, eight males with deviating morphology were excluded from the data. Five individuals had notably long wings (able to fly), which is known to have an effect on reproductive investment (Sakaluk, 1996). Two individuals had tegmena folded opposite the normal direction, and their wing morphology was overall very deviant. One male had very small female-like tegmena incapable of making calls.

Morphological measurements were used to form composite measures of size and fluctuating asymmetry. As the size of the individual is a sum of several morphologies, we summed morphological data in the first principal component (PC) out of pronotum width and tibia length (PC1 explained 77.19% of variation in size, with an eigenvalue of 1.54, while the correlation between PC1 and both variables was 0.879). We also extracted a principal component using unsigned fluctuating asymmetry of wing and tibia as components of global fluctuating asymmetry (PC1 explained 52.29% of variation in fluctuating asymmetry, with an eigenvalue of 1.046, while the correlation between PC1 and both variables was 0.723). These principal components were made to reduce the number of traits that are included in the analyses. This also removes the correlated characters and thus reduces the collinearity problem in logistic regression, increases the power of the logistic regression, reduces the problems associated with multiple comparisons, and simplifies the discussion. As an estimate of condition, we used residual mass extracted from a linear regression of mass on PC1 of size (i.e. the weight that is not explained by size). This measurement is supposed to reveal fat content and hence allocation ability of an individual. It is often used for this purpose, although there are problems with its interpretation (see Jacob *et al.*, 1996; Kotiaho, 1999).

Estimating selection

We estimated female preference on standardized male traits by using logistic regression. This method was chosen since female choice was a binary trait. Traits considered in the analysis were: courtship call rate, mean size of the harp, fluctuating asymmetry of harp, 'global fluctuating asymmetry' (PC1 of fluctuating asymmetry), body mass, condition, PC1 of size, and relatedness. In addition to these linear effects, we also included the quadratic effect of coefficient of co-ancestry in the analysis. This was done because the theoretical expectation is explicitly about non-linear selection on relatedness (Puurtinen *et al.*, 2005) – that is, a negative quadratic selection gradient. Regression coefficients were transformed to selection gradients according to Janzen and Stern (1998). We first considered the total data set by analysing mating success of all males. However, a dull fact is that silent males might not be successful. Therefore, we also estimated mating success among males that called. In both selection analyses, PC1 of size was excluded from logistic regression due to strong collinearity between other size-informing traits (weight and mean harp size).

Estimating variance components

To calculate genotypic and phenotypic variances and covariances for traits, we used an animal model and restricted maximum likelihood method (REML). This method fits a

linear mixed model to estimate variance components for continuous traits. In our case, individuals were raised individually from very early stages, and therefore the only explanatory variable was the identity of the individual, which was fitted as a random effect. The identity of the individual links data from all relationships of the interconnected pedigree and allows the estimation of phenotypic variation that is due to the coefficient of co-ancestry between individuals. In complex pedigrees, there is a variety of different relationships between individuals and hence this method is more powerful than traditionally employed methods for obtaining estimates of additive genetic variation (Lynch and Walsh, 1998).

Since data consisted of individuals from full sib families with additional relationships to members of other families, despite individual rearing, there is a possibility that family effects (e.g. common maternal effects or dominance effects) might cause inflation of estimated additive genetic variance (Lynch and Walsh, 1998). Thus, the family effect was included in the univariate analysis in addition to the additive genetic effects. Log likelihood ratio tests revealed that the inclusion of the family effect on the model did not improve model fit significantly, as statistical probabilities obtained from the χ^2-distribution ranged from 1 to 0.4. Hence further analyses were conducted without the family effects.

We continued the analysis by bivariate analyses, estimating variance and covariance components of two traits simultaneously. From these estimates, we calculated heritabilities (h^2) and genetic and phenotypic covariances (see Lynch and Walsh, 1998; Gilmour *et al.*, 2002). Statistical significance of the estimates was assessed by comparing the estimates to their standard errors. Because heritability cannot be less than zero (i.e. the null hypothesis is that heritabilities are not greater than zero), one-tailed tests were used in their significance testing. Genetic and phenotypic correlations were tested with two-tailed tests.

We did not measure the longevity of the test individuals. However, using their relatives reared in the laboratory in a comparable environment without manipulations, we were able to obtain estimates of additive genetic variance of longevity and genetic covariance between longevity and the other traits. In addition, we calculated estimates of evolvability of the traits as a coefficient of additive genetic variation (CV_A) (Houle, 1992; Lynch and Walsh, 1998).

RESULTS

Descriptive statistics of measured traits are given in Table 1. Based on the multivariate logistic regression analyses, the mating success of a male was clearly determined by his courtship call rate (Table 2; Fig. 1). We did not find any other traits significantly affecting male mating success. We analysed our data set also by considering only males that called. This did not change the results and courtship call rate was still the only determinant of male mating success (Table 2). In both analyses, the quadratic regression coefficient of relatedness on male mating success was high and negative as expected, but not significant.

There tended to be a weak positive phenotypic correlation between male courtship call rate and body mass (Table 3). Other traits did not correlate with courtship call rate. However, there were several highly positive correlations between various morphological traits. In addition, the size of the spermatophore's sperm-ampulla correlated positively with body mass and body size. The size of the nuptial gift measured as the weight of the spermatophore of the spermatophylax did not correlate with any of the measured traits (Table 4).

There was a relatively high heritability for harp size, PC1 of size, and longevity of males (Table 1). Heritability of female longevity was moderate, but not significantly different from

Table 2. Strength of sexual selection on male traits and relatedness between males and females (mean values with standard errors in parentheses)

	Logistic regression analysis					
	All males			Active males		
Trait	α	β_{avgrad}	*P*	α	β_{avgrad}	*P*
Courtship call rate	1.342	0.779	**<0.001**	1.375	0.716	**0.002**
	(0.384)	(0.223)		(0.434)	(0.226)	
Harp size (mm^2)	−0.260	−0.151	0.815	−0.736	−0.383	0.521
	(1.112)	(0.646)		(1.147)	(0.598)	
FA harp (mm^2)	−0.193	−0.112	0.561	−0.152	−0.079	0.669
	(0.331)	(0.192)		(0.356)	(0.186)	
FA global (PC1)	0.514	0.299	0.136	0.612	0.319	0.129
	(0.345)	(0.200)		(0.404)	(0.211)	
Body mass (mg)	−0.111	−0.065	0.929	0.661	0.344	0.612
	(1.235)	(0.718)		(1.303)	(0.679)	
Condition (RBM)	−0.333	−0.194	0.598	−0.638	−0.333	0.331
	(0.633)	(0.367)		(0.657)	(0.342)	
Relatedness ($\theta_{m,f}$)	20.579	11.95	0.075	19.28	10.05	0.122
	(11.571)	(6.724)		(12.48)	(6.508)	
Relatedness $(\theta_{m,f})^2$	−5.311	−3.086	0.094	−4.767	−2.484	0.163
	(3.180)	(1.848)		(3.420)	(1.783)	
Intercept	2.691	1.132	0.121	2.119	1.105	0.180
	(1.460)	(0.848)		(1.582)	(0.824)	
Model statistics:	$N_{total}/N_{chosen} = 74/31$			$N_{total}/N_{chosen} = 64/29$		
	$R^2_{Cox\ \&\ Snell} = 0.277, R^2_{Nagelkerke} = 0.372$			$R^2_{Cox\ \&\ Snell} = 0.288,\ R^2_{Nagelkerke} = 0.385$		

Note: Values were estimated from all males and only from those males that called (active males) with logistic regression on female preference. Logistic regression coefficients were transformed to linear selection gradients (β_{avgrad}) as described in Janzen and Stern (1998). The linear selection gradient on relatedness $(\theta_{m,f})^2$ equals the quadratic selection gradient (i.e. γ-gradient). A negative quadratic selection gradient indicates stabilizing selection. This convex selection indicates that intermediate trait values are associated with higher positive selection. FA = fluctuating asymmetry, RBM = residual body mass.

zero. Condition, measured as residual mass, and weight were moderately heritable, while both courtship call rate and global asymmetry had only a small amount of heritable variation and were not significantly different from zero (Table 1). Fluctuating asymmetry of harp possessed zero variance when analysis was bound not to produce negative variance components (Table 1). When negative variance components were allowed, fluctuating asymmetry of the harp showed a negative variance component (−0.179, standard error = 0.094). This estimate is presented, although the expectation is that variance cannot be negative, because reporting just zero heritability might bias future meta-analyses to a more positive direction (Kotiaho and Tomkins, 2002; Tomkins and Kotiaho, 2004). Negative variance components are commonly found if data analysis is done on rather small data sets. This means that real variance components are small but estimates converge to negative values (Lynch and Walsh, 1998).

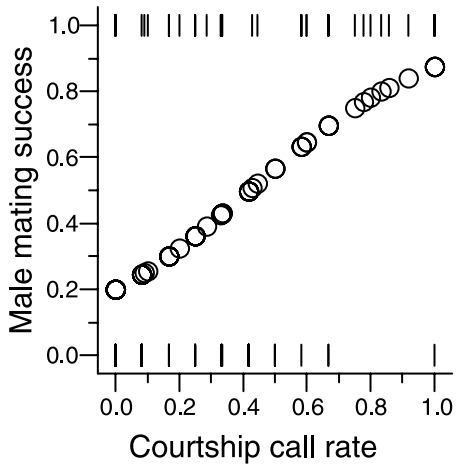

Fig. 1. Effect of courtship call rate on female preference. Ticks indicate male courtship call rate and circles indicate predicted values of logistic regression of male courtship call rate on female preference.

Strong positive genetic correlations existed between size-related traits and between harp size and male longevity (Table 3). Courtship call rate, condition (measured as residual mass), and global fluctuating asymmetry were not genetically correlated with any of the traits (Table 3). Note that the negative estimate of additive genetic variance of harp fluctuating asymmetry precludes the calculation of genetic correlations. A negative estimate of variance also prevented standardization of variation by mean (Houle, 1992). Moreover, our results also pinpoint the difficulties of this kind of standardization, as they rely on many assumptions (see Lynch and Walsh, 1998, ch. 11). For example, the relationship between variance and mean is expected to be linear and to intercept the origin, which is not the case in composite measures such as principal components (Table 1).

DISCUSSION

By exploring several potential male traits that could affect male mating, we found that male mating success was clearly and mostly explained by male courtship call rate. In contrast to several other cricket studies (see below), we examined whether, in addition to acoustic signalling, other cues might affect mate choice. In the present study, popular compatibility choice was not found to be significantly involved in mate choice. The previously common expectation of fluctuating asymmetry affecting male success was not supported either. Potential other traits such as size, weight, and condition measured as residual mass did not have an effect on mate choice. Moreover, we did not find clear evidence for any benefits to be associated with female choice: spermatophylax size was not correlated with sexual signals, and we did not find evidence for heritable attractiveness or a genetic correlation between attractiveness and components of fitness. It is possible that some other, here unmeasured, trait confers benefits or that immaterial direct benefits such as a species-specific sexual signal may be beneficial enough to drive mate choice in this system. Another possibility is that the cost of expressing attraction towards males may be so small that the benefits needed to outweigh the costs are minute and cannot be observed with the sample sizes in our data set.

Table 3. Phenotypic and genetic correlations with standard errors of estimates (in parentheses) and their statistical significance between measured traits

	Courtship call rate	Harp size	FA global	Weight	Condition (RBM)	Size	FA harp
Courtship call rate	—	−0.0005 (0.118) $P = 0.968$, $n = 85$	−0.046 (0.123) $P = 0.711$, $n = 75$	0.178 (0.102) $P = 0.084$, $n = 107$	0.199 (0.112) $P = 0.075$, $n = 88$	0.033 (0.116) $P = 0.779$, $n = 90$	−0.067 (0.109) $P = 0.543$, $n = 85$
Harp size	−0.511 (0.447) $P = 0.162$	—	−0.0063 (0.124) $P = 0.960$, $n = 86$	**0.712 (0.056)** **$P < 0.001$, $n = 94$**	0.210 (0.112) $P = 0.059$, $n = 94$	**0.678 (0.065)** **$P < 0.001$, $n = 96$**	−0.169 (0.102) $P = 0.099$, $n = 96$
FA global	0.006 (0.594) $P = 0.920$	−0.194 (0.443) $P = 0.660$	—	−0.047 (0.118) $P = 0.697$, $n = 86$	0.058 (0.119) $P = 0.999$, $n = 86$	−0.091 (0.120) $P = 0.453$, $n = 87$	−0.011 (0.109) $P = 0.920$, $n = 87$
Body mass	0.257 (0.474) $P = 0.589$	**0.709 (0.201)** **$P < 0.001$**	−0.377 (0.434) $P = 0.395$	—	**0.452 (0.089)** **$P < 0.001$, $n = 100$**	**0.874 (0.026)** **$P < 0.001$, $n = 100$**	0.014 (0.102) $P = 0.886$, $n = 95$
Condition (RBM)	−0.734 (0.523) $P = 0.162$	0.206 (0.419) $P = 0.689$	0.229 (0.503) $P = 0.653$	0.224 (0.403) $P = 0.582$	—	−0.032 (0.115) $P = 0.787$, $n = 100$	−0.089 (0.102) $P = 0.384$, $n = 95$
Size	0.344 (0.481) $P = 0.484$	**0.686 (0.202)** **$P < 0.001$**	−0.589 (0.388) $P = 0.121$	**0.895 (0.084)** **$P < 0.001$**	−0.146 (0.422) $P = 0.734$	—	0.041 (0.102) $P = 0.697$, $n = 95$
Longevity	0.467 (0.424) $P = 0.271$	0.523 (0.329) $P = 0.134$	0.309 (0.405) $P = 0.447$	0.167 (0.376) $P = 0.667$	−0.017 (0.455) $P = 0.976$	0.195 (0.355) $P = 0.596$	—
Longevity, males	0.612 (0.467) $P = 0.194$	**0.918 (0.385)** **$P = 0.005$**	0.505 (0.469) $P = 0.317$	0.253 (0.482) $P = 0.603$	−0.770 (0.522) $P = 0.156$	0.272 (0.454) $P = 0.555$	—
Longevity, females	0.428 (0.559) $P = 0.447$	0.467 (0.407) $P = 0.254$	0.244 (0.506) $P = 0.631$	0.134 (0.466) $P = 0.779$	0.025 (0.543) $P = 0.968$	0.179 (0.441) $P = 0.653$	—

Note: n = sample size in correlations. Above the diagonal are phenotypic correlations and below the diagonal are genetic correlations. Phenotypic correlations could not be estimated between longevity and other traits, since longevity was measured from relatives (i.e. in different individuals than the other traits). Since the estimate of additive genetic variation of harp fluctuating asymmetry was negative, or zero if analysis was bound to produce variance components that are within a theoretical parameter space, the calculation of genetic correlations between harp fluctuating asymmetry and that of the other traits was not possible. Statistical significance of the genetic correlations was tested with two-tailed tests. Significant correlations are highlighted in **bold**. FA = fluctuating asymmetry, RBM = residual body mass.

Table 4. Correlations (r) and their significance (P) between sperm ampulla and spermatophylax of the spermatophore and other measured traits

	Ampulla	Spermatophylax
Ampulla	—	$r = 0.027$, $P = 0.879$, $n = 35$
Spermatophylax	$r = 0.027$, $P = 0.879$, $n = 35$	—
Courtship call rate	$r = -0.244$, $P = 0.129$, $n = 40$	$r = 0.166$, $P = 0.363$, $n = 32$
Harp size	$r = 0.252$, $P = 0.150$, $n = 34$	$r = 0.266$, $P = 0.188$, $n = 26$
FA harp	$r = -0.074$, $P = 0.671$, $n = 35$	$r = -0.059$, $P = 0.771$, $n = 27$
FA global	$r = 0.226$, $P = 0.222$, $n = 31$	$r = 0.206$, $P = 0.334$, $n = 24$
Body mass	$r = 0.209$, $P = 0.179$, $n = 43$	**$r = 0.428$, $P = 0.011$, $n = 34$**
Condition (RBM)	$r = -0.247$, $P = 0.141$, $n = 37$	$r = 0.230$, $P = 0.239$, $n = 28$
Size	$r = 0.265$, $P = 0.108$, $n = 38$	**$r = 0.477$, $P = 0.009$, $n = 29$**

Note: Significant correlations are highlighted in **bold**. FA = fluctuating asymmetry, RBM = residual body mass.

Male *G. sigillatus* mating success was strongly affected by courtship call rate. Our results in this respect do not differ from much of the literature, as acoustic signals are commonly found to attract crickets (e.g. Loher and Dambach, 1989). This is the case, for example, with *Gryllus integer* (Hedrick, 1986; Gray and Cade, 1999), *Gryllus lineaticeps* (Wagner and Reiser, 2000; Wagner and Basolo, 2007), and *Teleogryllus commodus* (e.g. Brooks *et al.*, 2005; Bentsen *et al.*, 2006). However, a large proportion of the published studies, including those cited above, do not consider or measure cues other than acoustic signals that could be used in female mate choice.

In addition to courtship call rate, another possible avenue for acquiring information about male quality is through song properties; it has been suggested that the quality of the sound can be affected by the morphology (e.g. symmetry) of the primary sound radiators (Simmons and Ritchie, 1996). However, we found no indication of harp morphology, such as asymmetry or size, affecting male mating success. This is in contrast to a study on *Gryllus campestris* in which females preferred calling songs with pure tones of low carrier frequency common to large and symmetrical harps (Simmons and Ritchie, 1996). However, it is worth noting that we did not analyse courtship song components directly, as did for example Rantala and Kortet (2003) with *Gryllus bimaculatus*, and thus are unable to relate the morphology to the song quality. We found no indication that direct visual cues such as size, condition, weight or overall asymmetry would have an effect on male mating success.

As well as acoustic and visual cues, information may also be mediated through pheromonal cues: pheromones may also reveal relatedness or social status (e.g. Moore *et al.*, 1997) in crickets, as in *Gryllus bimaculatus* (Simmons, 1989) and *Gryllus integer* (Kortet and Hedrick, 2005). Provided that pheromonal cues can reveal relatedness between males and females, evolution of the preference for optimal outbreeding (i.e. avoiding inbreeding and outbreeding) might

be possible (Neff and Pitcher, 2005; Puurtinen *et al.*, 2005). However, we found no support for this hypothesis, as the required negative quadratic selection gradient was non-significant, although high. Nevertheless, in field crickets *Gryllus bimaculatus*, Simmons (1989) found that females indeed mated sooner with males that were non-related, suggesting a role for pheromones. However, to maintain its viability, our cricket population was relatively outbred, yielding low mean and variance in the degree of relatedness between assessed males and females. This may cause estimation inaccuracy in regression analysis but also during mate choice, since selection for compatibility might be restricted to very simple and coarse rules of thumb such as familial imprinting (Penn and Potts, 1998; Hurst *et al.*, 2005; Puurtinen *et al.*, 2005). In fact, there is also some evidence that *G. sigillatus* females may use simple self-reference cues in mate choice (Ivy *et al.*, 2005).

Pairing with males possessing a strong heritable sexual signal, females may benefit by having attractive sons or, if the sexual signal is also genetically correlated with viability or some other component of genetic quality, also by increased offspring fitness. However, we found non-significant heritability of courtship call rate and no genetic correlation between courtship call rate and any of the quality surrogates such as condition, weight or longevity. It should be noted that courtship call rate contained a moderate amount of heritable variation, albeit statistically non-significant, with this sample size. It is also worth noting that we, like most others, are examining only components of fitness such as condition or longevity. Even though condition and longevity might be selectively important traits, these alone are not equal to the total fitness on which the selection is supposed to act on (Hunt *et al.*, 2004).

Morphological traits such as mean harp size, size (PC1), and weight had relatively high and significant heritabilities. In addition, our surrogate of condition, the residual body mass, possessed a moderate amount of heritable variation. Heritability of morphological traits (e.g. size) is normal, but perhaps more uncommon is the high heritability of longevity. This finding is most likely due to controlled laboratory rearing, since the causes of death in the wild are often random and hence easily yield non-significant heritability estimates (Price and Schluter, 1991). Our results are in line with several other recent studies that have found fluctuating asymmetry to be non-heritable (e.g. Blanckenhorn and Hosken, 2003; Kruuk *et al.*, 2003).

Low heritability can be due to low additive genetic variance or high residual variance if phenotypic variance consists mostly of environmental or non-additive genetic variance (Price and Schluter, 1991; Merilä and Sheldon, 1999). Indeed, the standardization of variance components has shown that there is a comparable or even higher amount of additive genetic variance in life-history traits than in morphological traits (Houle, 1992; Pomiankowski and Møller, 1995). Our study revealed similar results, as the moderately but non-significantly heritable courtship call rate had a higher CV_A than highly heritable morphological traits. However, even if there is a large amount of additive genetic variation in the trait, and hence potential for selection, it is useless for females, in terms of obtaining genetic benefits, if a large amount of residual variance masks it.

Despite the obvious benefits of controlled laboratory rearing environments (e.g. enabling the construction of a pedigree), laboratory rearing can also have unwanted effects on results. The most common concern is how laboratory rearing affects variance components and hence heritability estimates. Controlling for environment might cause inflation of heritability estimates in the laboratory due to a reduction of the environmental variance. However, an opposite effect can be found if *ad libitum* food allows individuals with poor

quality to compensate their trait expression in the laboratory, causing reductions in the visibility of the genetic effects. However, there is no general consensus as to the direction of the bias (Lynch and Walsh, 1998). Another potential bias that might arise due to laboratory rearing and controlled mating is persistence of genetic correlations in the absence of sexual selection, especially if the genetic correlation is due to gametic phase disequilibrium. Then, depending on the recombination frequency between loci, the correlation might disappear after one or a few generations of relaxed selection (Lynch and Walsh, 1998). Moreover, the lack of significant heritabilities or correlations could be due also to the size of our data set, which may not have had the power to detect the expected (Kirkpatrick and Barton, 1997) and generally found (Møller and Alatalo, 1999; Qvarnström *et al.*, 2006) low good genes effects.

In contrast to strict requirements involved in acquiring genetic benefits via pre-mating selection, the direct benefits require only positive phenotypic correlation between signal intensity and benefit. Examples of these kinds of benefits might be territorial quality or nuptial gifts (e.g. Andersson, 1994). *Gryllodes sigillatus* males produce a large spermatophore consisting of sperm ampulla and large gelatinous spermatophylax. During sperm transfer after mating, the female consumes this spermatophylax. These kinds of spermatophores are frequently suggested to offer energetic (Vahed, 1998) or hydration (Ivy *et al.*, 1999) benefits to females. Thus, a strong sexual signal could convey information about size of these nuptial gifts to a female (e.g. Ivy *et al.*, 1999). However, we found no evidence of this kind of direct benefit: there was no correlation between size of the nuptial gifts and courtship call rate.

In addition to the normally considered benefits mediated, for example, via nuptial gifts or via genetic effects, the females may benefit directly from the male signal itself. Such a benefit could be due to reduced mate searching costs mediated by the phonotaxis (Hack, 1998; Kokko and Mappes, 2005), although in this study we only examined courtship call rate that is used for the final courtship prior to mating in close proximity. However, strong species-specific phonotaxis may be beneficial via avoidance of maladaptive hybridization (Dobzhansky, 1951; Sætre *et al.*, 1997). These kinds of benefits are available by simply responding after any conspecific signal and thus are likely to be relatively cost free. This kind of sensory trap can also lead to sexual conflict via post-copulatory exploitation or non-optimal mating rates (Holland and Rice, 1998), underpinning the negative aspects of sensory exploitation/bias. However, this is determined by how mate- or sperm-limited females are (e.g. Kokko and Mappes, 2005; Kokko and Rankin, 2006). Nonetheless, if there are no additive genetic benefits available, and as non-additive benefits are practically impossible to predict (Puurtinen *et al.*, 2005), the other way to obtain genetic benefits might be to mate multiple times and acquire genetic benefits through post-copulatory choice. This is exactly what Ivy and Sakaluk (2005) found in their recent study with the same species: polyandry conferred genetic benefits in terms of increased offspring survival. Thus, male sexual signalling in this species might just facilitate mating and ensure the species of potential mating companions and, therefore, is beneficial on its own.

To summarize, our results show that there appears to be directional sexual selection on male signalling, and the lack of clear benefits corresponds to the lek-paradox in the traditional sense: why females tend to choose if there is apparently nothing to be gained. Three resolutions were offered for resolving this paradox: sexy sons, good genes, and direct benefits (Kirkpatrick and Ryan, 1991). We did not find clear evidence for good genes sexual selection, or direct benefits mediated via size of nuptial gifts. Lack of genetic benefits may be due to relatively low power to detect small benefits. However, it should be remembered

that females might benefit directly from the signal itself by facilitating mating *per se*, more than they might lose if not responding to the species-specific courtship call.

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