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Sexual selection in the cricket *Gryllus bimaculatus*: no good genes?

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Abstract Recent studies have suggested that females of the field cricket *Gryllus bimaculatus* exercise post-copulatory choice over the paternity of their offspring. There is evidence that these choices are made in relation to the genetic compatibility of mates rather than their absolute quality, but the magnitude of heritable differences in males has not been thoroughly examined. Using a half-sib breeding design we measured additive genetic variance and dam effects in a suite of reproductive and non-reproductive traits. Both components explained relatively little of the phenotypic variance across traits. The dam component in our design contains variance caused by both maternal effects and dominance. If maternal effects are negligible as suggested by previous studies, our data suggest that dominance variance is an important source of variation in these traits. The lack of additive genetic variation, but possible existence of large amounts of non-additive genetic variation is consistent with the idea that female mate choice and multiple mating may be driven by differences in genetic compatibility between potential mates rather than by differences in genetic quality.

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Introduction

Why selection for traits conferring a mating advantage does not rapidly exhaust additive genetic variation in such traits remains a major question in evolutionary genetics (Pomiankowski and Møller 1995; Rowe and Houle 1996). In a previous study of the field cricket *Gryllus bimaculatus*, a model system for studies of sexual selection (Simmons 1986, 1987a; Sakai et al. 1991; Adamo and Hoy 1994; Tregenza and Wedell 1997, 1998, 2002; Bateman 1998; Tachon et al. 1999; Bateman et al. 2001; Morrow and Gage 2001; Bretman et al. 2004; Bretman and Tregenza 2005), individuals that were more successful in obtaining matings had sons who were also better at gaining matings although they experienced longer development times, a trait presumably under directional natural selection (Wedell and Tregenza 1999). If males can trade-off sexually selected and naturally selected traits then females that choose the most attractive males may simply be getting males that have diverted investment into sexual traits rather than males that carry absolutely better genes, which will weaken benefits of female choice.

Male field crickets produce calling song to attract females, and wild females generally mate with several males, and are typically found carrying sperm from a number of previous mates (Bretman and Tregenza 2005). There is no evidence for last male sperm precedence (Simmons 1987c) but females appear to benefit from polyandry through genetic benefits to their offspring (Tregenza and Wedell 1998). There is evidence that this may be because females

avoid using sperm from closely related males (Tregenza and Wedell 2002; Bretman et al. 2004), but there remains the possibility that genetic differences between males mean that some individuals confer higher viability on their offspring regardless of their mate. We examine this possibility by determining the extent of additive genetic variance for fitness related traits.

The concept of condition dependence (see Tomkins et al. 2004 for review) assumes that organisms have a pool of resources with which to build their traits, and hence there will be trade-offs between traits that bring increasing fitness benefits with increasing investment, with the crucial assumption that the costs of a marginal increase in the size of a condition dependent trait are lower for individuals in better condition. Sexually selected traits are expected to show strong condition-dependence because they are costly to produce and hence there should be positive correlations between such traits. We test this prediction in *G. bimaculatus*, obtaining phenotypic correlations between six male sexually selected traits.

Materials and methods

Experimental design

To capture as much of the standing genetic variation as possible, we collected three females (grandmothers) and a large number of males from two sites <14 km apart near the Doñana National Park in Sevilla, Spain at Espartinas and Aznalcázar.

These sites are home to a very large population of this species numbering in the thousands, making it very unlikely that any of our collected crickets would be close relatives. The three grandmothers were collected in May 2002, they had mated in the wild and additionally were each mated in the laboratory with at least three randomly selected males collected at the same time as the females in order to increase genetic variability in their offspring. Female offspring from these three grandmothers were then used as the dams in our quantitative genetic design—these dams had an average relatedness of 0.3 within a female line (assuming five fathers per brood, Bretman and Tregenza 2005) and zero between lines, giving an average of around $r = 0.1$. Dams were mated with a new group of wild males (sires) from the same wild population collected in July 2002. Field crickets have an X-O sex determination system which does not involve any exclusive male or female chromosomes, hence our design using three initial female founders but a large number of males and all independent wild caught males for the parental generation will only cause a very slight reduction in genetic variability (about 5%) of parental stocks in comparison to using individuals immediately captured from the wild. This method provides greater confidence in the retention of genetic variation than is possible when using a mass reared laboratory population.

We adopted a full-sib half-sib design (Lynch and Walsh 1998) using 25 wild caught males and 75 laboratory reared females. This design allowed us to partition phenotypic variance into dam and sire components. Every male was mated (twice) with each of three unrelated virgin females (one daughter from each of the three initial wild females), to produce 75 families. There was no intermediate lab generation, so adaptation to the lab could only occur through differential mortality in a single generation of dams. After mating, females were isolated and provided with food pellets (Rat and Mouse Diet, B and K Universal, Hull, UK) and wet sand for oviposition. Eggs were collected daily until around 200 eggs per female were laid, and incubated in two independent groups of around 100 eggs on a piece of wet sponge cloth at 28.5°C until all of them either hatched or died. Hatchlings from each family were reared in two independent plastic boxes ($30 \times 21 \times 13$ cm^3) at a maximum initial density of 40 nymphs per box (lower densities were used for a few females producing fewer than 40 nymphs). Boxes were provided with excess food and water, and moved around the constant temperature room every few days in case there were thermal gradients within the room. The room was maintained at 28.5°C at all times with an 18:6 ratio of light to darkness. Developing nymphs were checked daily until all of them either reached adulthood or died. To ensure all adults were virgin, nymphs were redistributed between the two boxes as soon as they could be sexed, so that each family had one box containing females and one containing males and unknown sex. This protocol is necessary because nymphs kept in isolation develop much slower (personal observation) but it does mean that there are differences in the density of family members experienced by different individuals at particular times which may introduce environmental noise. We attempted to minimise any effects of this sort by providing food and water in excess at all times. Subsequently, newly observed females were transferred to the female only box. Within 24 h of emergence, adults were transferred to individual plastic boxes ($9 \times 9 \times 5$ cm^3) provided with excess food and water. They were reared in that box until natural death occurred. Adult boxes were checked for dead crickets at 12–48 h intervals.

Study traits

We measured as many fitness and sexually selected traits (Table 1) as possible, provided that a minimum of four offspring per sex and family could be processed. For all the families, we measured hatching success and survival to

Table 1 Traits included in the study

Code	Trait	Mean ± SD	N
Hs	Average hatching success (average proportion of eggs surviving to hatch)	0.64 ± 0.14	49
As	Adult survival (proportion of nymphs surviving to adulthood)	0.23 ± 0.10	49
FTw	Female thorax width (mm)	7.3 ± 0.6	643
FDt	Female developmental time (day)	58.9 ± 19.1	664
FLs	Female lifespan (day)	45.6 ± 18.8	653
FFe	Female average fecundity	74.9 ± 48.5	280
FEm	Female average dry egg mass (mg)	0.22 ± 0.02	261
FHd	Female average hatchling dry mass (mg)	0.18 ± 0.02	263
MTw	Male thorax width (mm)	7.0 ± 0.8	536
MDt	Male developmental time (day)	54.2 ± 13.7	549
MLs	Male lifespan (day)	42.2 ± 17.6	539
Mt	Time until mating from putting male and female together (h)	0.26 ± 0.40	317
MLt	Time between consecutive matings (after the mating measuring Mt) (h)	1.30 ± 0.50	317
MSm	Spermatophore dry mass (mg)	1.86 ± 0.41	251
MFa	Male fighting ability (number of fights won from four contests)	2.23 ± 1.29	284
MCd	Male calling duration within a 24 h period (h)	1.28 ± 1.97	286
MFe	Average fecundity from the female the male mated with	75.7 ± 48.8	267
MEm	Average egg dry mass from the female the male mated with (mg)	0.22 ± 0.02	248
MHd	Average hatchling dry mass from the female the male mated with (mg)	0.18 ± 0.02	254

adulthood and for all the individuals surviving to adulthood, body size (thorax width), development time and adult lifespan. To measure female reproductive parameters, female offspring were mated twice with a single unrelated male at an average age of 9.0 ± 1.7 days [mean ± standard deviation (SD)]. After mating, they were provided with wet sand for oviposition. Fecundity was expressed as the average number of eggs laid per day over the initial 2 weeks after mating (13.9 ± 1.82 days). Egg mass was calculated by drying and weighing a sample of around 15 eggs collected a few days after mating (time from mating to collection 4.82 ± 0.69 days). Samples of a maximum of 100 eggs (depending on the female's fecundity) were incubated until hatching. A maximum of ten hatchlings were collected within the first 24–48 h after hatching, dried and weighed. During the period before being collected, hatchlings had access to water but not food. Those waiting to be dried for more than 24 h were kept at 20°C to minimise the rate of mass loss.

To measure male reproductive parameters, males were mated twice with the same female at an age of 8.32 ± 3.79 days. The male and female were placed together in a circular arena of 10 cm diameter with a fresh piece of filter paper on the floor. We measured the time from when pairs were placed together until the first spermatophore was attached to the female (Mt), and then the time between the first and the second spermatophore attachments (MLt). Male–male competition trials (fights) were conducted over four consecutive days starting the day after mating. The target male was marked with a small spot of correction fluid and sequentially confronted with four males from another stock population at ~24 h intervals, which has been shown to remove the effects of the previous contest on the cricket behaviour (Khazraïe and Campan 1999) see (Bretman et al. 2006) for details of methods. On rare occasions (10/1120 bouts) when no fight occurred both crickets were removed and a new opponent was assigned 24 h later.

The winner of a fight was easily determined (Adamo and Hoy 1995). Once males meet head to head, they begin to batter each other with their antennae. They then open their mandibles fully and engage, locking jaws and pushing their opponent. After they release mandibles, the loser will be chased and the winner will call. Often one male will call when another is detected. This was not taken as winning a fight. To determine an outright win, there either had to be a head to head fight resulting in chasing, or one cricket consistently chased and harassed another. After the winner had been established, crickets were removed immediately. Every fight was scored zero when lost by the target male and one when the target male won, thus total score ranged between zero and four.

The day after the last fight, the male was introduced into a soundproof chamber during the light period of the day, within a small wire cage provided with food and water. Singing activity was automatically recorded every second for 24 h, and the result expressed as time spent singing. Spermatophore mass was estimated from a spermatophore

removed using forceps from the male genetalia at an age of 23.3 ± 9.91 days (this procedure is non-invasive and does not harm males). There is abundant evidence that male insects can influence the reproductive investment made by their mates (Chen et al. 1988; Ashworth and Wall 1994; Herndon et al. 1997; Heifetz et al. 2000; Czesak and Fox 2003). To assess whether male crickets have heritable traits that can influence female reproductive output we measured the egg mass, fecundity and hatchling size of females to which particular males had mated and analysed these traits as being properties of both males and females.

Data analyses

A number of females failed to produce eggs, offspring or adults, and some adults died before all traits were measured, yielding an unbalanced data set. In particular, 12 males only produced offspring with a single dam, meaning that these offspring contributed little to variance component estimation. A restricted maximum likelihood approach was employed using ASReml (NSW Agriculture, Orange, NSW, Australia), which is appropriate for situations where data are imbalanced (Lynch and Walsh 1998). We also conducted analysis of variance tests of a balanced sub-set of the data which gave qualitatively identical results (not shown). To estimate variance components we used a random effects linear model:

$$z = \mathrm{Xu} + a + Zd + e,$$

where **z** is the vector of measured trait values and X is the design matrix for the fixed effects and u the associated parameters. **a** is a vector of breeding values and **d** a vector of effects for each dam. The design matrix **Z**, relates each individual to their respective mothers and **e** is a vector of residuals. Both the residuals, and the dam effects are assumed to be independently distributed. Breeding values are not independently distributed due to family structure and are normally distributed with mean zero and (co)variance structure $\sigma^2_{\mathrm{A}}A$ where σ^2_{A} is the additive genetic variance and **A** is the matrix of relationship coefficients. Dams originating from the same mother were assumed to be half-siblings, and the relationship matrix **A** was modified accordingly. Standard errors for all variance component functions were calculated using the Delta method (Lynch and Walsh 1998).

Estimates of σ^2_{A} are confounded with environmental paternal effects in this design, however, unlike some crickets, male *G. bimaculatus* produce only a small spermatophore that does not have any known direct effects on offspring fitness (Simmons 1988a). Therefore, paternal nutrient effects are unlikely and we assume that this term is dominated by additive genetic effects. The dam component (σ^2_{Dam}) contains variance due to maternal effects and a common rearing environment (σ^2_{M}) and also a quarter of the dominance genetic variance (σ^2_{D}). Common environment effects are reduced by our rearing protocol, which used two independent boxes per family during the nymphal period and an independent box per individual during the adult period. In the absence of common environmental and maternal effects an estimate of dominance variance is $4 \times \sigma^2_{\mathrm{Dam}}$.

Results and discussion

For the set of traits that we measured, we did not find any evidence supporting the existence of males with good genes that could bring benefits to all their mates. Additive genetic effects explained relatively little phenotypic variance for most traits (Table 2), although the standard errors on these estimates were large. The dam component was of comparable magnitude, which may imply a large dominance component if maternal and common environmental effects are absent. Our finding of very low standing genetic variation for the traits we examined (Table 2) cannot simply be dismissed, despite the fact that it runs contrary to the large number of studies that find significant heritabilities in fitness related life history and sexually selected traits (Houle 1992; Pomiankowski and Møller 1995; Lynch and Walsh 1998). A benign laboratory environment has the potential to reduce the expression of additive variance, especially for traits related to condition. Determining whether our lab environment is either benign or hostile is not straightforward. However, if it is either substantially more benign or hostile than the natural environment, differences may arise in adult size between crickets growing in the wild and the lab. Comparing the size of a sample of wild males with a random sub-sample of our laboratory males we did not find any significant difference (ANOVA $F_{1,40} = 0.050$; $P = 0.82$). Combined with the fact that large numbers of broods failed to complete development in the lab, this suggests that our laboratory environment is not particularly benign.

It appears that our population shows low levels of additive genetic variance, following theoretical expectation (because selection and drift should erode genetic variation), but a larger study would be required to test whether additive genetic variance is absent in the relevant dimensions (Mezey and Houle 2005). Such a situation would suggest that females in this population cannot use pre or post-mating choice to acquire ‘good genes’ for their offspring. We cannot determine whether variance has been lost primarily through selection or drift. Population genetic data for this species are lacking, but it is possible that population bottlenecks occur during harsh winters or other periodic events, which could be evolutionarily significant.

Table 2 Narrow sense heritabilities and variance components (SE) expressed as the proportion of the phenotypic variance

Trait	Fixed	Dam	Residual	h^2	Transformation
Hs					
As					
Tw	Sx 0.286 (0.040)**	0.049 (0.039)	0.871 (0.060)	0.080 (0.084)	–
Dt	Sx 0.063 (0.014)**	0.124 (0.059)*	0.839 (0.071)	0.036 (0.112)	log
Ls	Sx 3.477 (1.059)**	0.025 (0.026)	0.947 (0.036)	0.027 (0.053)	–
FFe	Ftw 0.027 (0.004)**	0.190 (0.086)*	0.771 (0.103)	0.040 (0.160)	sqrt
FEm		0.113 (0.112)	0.706 (0.186)	0.181(0.231)	×100
FHd		0.075 (0.051)	0.925 (0.110)	0.000 (–)	×100
Mt					
MLt		0.003 (0.006)	0.974 (0.144)	0.000 (–)	log(×100)
MSm	Age 0.021 (0.002)**	0.020 (0.085)	0.851 (0.167)	0.129 (0.171)	–
MFa	MTw0.733 (0.086)**	0.009 (0.073)	0.769 (0.164)	0.222 (0.162)	–
MCd		0.088 (0.050)	0.912 (0.101)	0.000 (–)	log
MFe	FTw 0.022 (0.005)**	0.224 (0.128)	0.736 (0.152)	0.040 (0.240)	sqrt
MEm		0.000 (–)	0.831(0.185)	0.169 (0.108)	×100
MHd		0.018 (0.090)	0.922 (0.173)	0.060 (0.169)	×100

Several traits were not normally distributed and had to be transformed prior to analysis. A normalising transformation could not be found for mating time (*Mt*) and it was not analysed. In models that included both sexes, the sex effect (*Sx*) is the difference between female and male intercepts. For these models F(female) and M(male) have been omitted from the trait codes presented in Table 1

Significance values are indicated by asterisks: $*P < 0.05$, $**P < 0.01$

Our experimental design does not allow dominance variance to be separated from common environment effects and maternal effects, but the experimental design should minimise these effects: broods were split and all individuals were reared under identical conditions with food and water provided in excess, density was controlled as much as possible, with nearly all boxes starting with 40 nymphs. Further work is needed to asses the magnitude of dominance variance in these traits, but it should be noted that if maternal and common environmental effects can be discounted, this study suggests dominance variance may great (4 × dam component in Table 2). Large dominance components are expected for traits closely linked to fitness (Merila and Sheldon 1999), and this has empirical support (Crnokrak and Roff 1995). Perhaps partly because there is no straightforward way of dealing with it from an analytical point of view, non-additive variance has historically been assumed to be negligible and unimportant for evolution (Falconer and Mackay 1996). There is growing interest in the importance of epistatic and dominance effects (Wade 2002), but still, many quantitative genetic studies, including studies of crickets, assume low non-additive variance and estimate heritability from the covariance between full siblings (Simons and Roff 1994; Grill et al. 1997; Christe et al. 2000; Bégin and Roff 2002; Réale and Roff 2002). Full-sib designs confound dominance and common environment effects with additive genetic effects, and may potentially lead to greatly inflated estimates of heritability. Strong fitness effects of interactions between genomes will increase the potential for polyandry and mate choice to be driven by genetic compatibility, but there remains the difficult question of how more compatible genotypes are recognised (Tregenza and Wedell 2000). Our sample sizes were prohibitively small for the calculation of genetic correlations, which require at least several hundred families to provide useful levels of accuracy (Lynch and Walsh 1998).

Tables 3, 4 show phenotypic correlations. Larger females took longer to develop, were more fecund and had heavier nymphs despite their eggs not being significantly heavier. Longer development times were associated with shorter lifespan, lower fecundity and lower egg mass, but also with higher dry mass of nymphs. As would be expected, heavier eggs produced heavier nymphs. Females that lived longer laid heavier eggs, and laid them faster. Larger males were more successful in fights and produced larger spermatophores, a trait which was also associated with shorter development time and longer lifespan. There was a very strong correlation between how long a male took before he would mate with the first female he encountered and how long he needed before he could remate. There was no significant correlation between egg hatching success and proportion of individuals surviving to adulthood ($r = 0.14$, $P = 0.35$, $N = 48$). Male traits with the potential to affect their mating success, and with potential roles in female choice include size (MTw),

Table 3 Phenotypic correlations within individuals (upper diagonal) and sample size (lower diagonal) for females

	FTw	FDt	FLs	FFe	FEm	FHd
FTw		0.17***	0.07	0.21	0.00	0.24***
FDt	643		–0.11**	–0.21***	–0.16**	0.39***
FLs	641	653		0.17	0.13	–0.01
FFe	271	280	277		0.12	–0.11
FEm	252	261	258	261		0.33***
FHd	254	263	260	231	221	

Significant values (without correction for multiple tests) are indicated by one to three asterisks for *P*-values below 0.05, 0.01 and 0.001, respectively

Table 4 Phenotypic correlations within individuals (upper diagonal) and sample size (lower diagonal) for males

	MTw	MDt	MLs	Mt	MLt	MSm	MFa	MCd
MTw		0.08	0.05	–0.04	–0.03	0.27***	0.46***	0.10
MDt	536		0.03	–0.10	0.03	–0.38***	0.01	–0.02
MLs	535	539		–0.06	–0.02	0.32***	–0.01	0.05
Mt	311	317	312		0.81***	–0.02	0.07	–0.08
MLt	311	317	312	316		–0.01	0.04	–0.08
MSm	245	251	246	249	250		0.03	0.05
Mfa	278	284	279	282	283	243		0.10
MCd	279	286	280	277	277	237	260	

Significant values (without correction for multiple tests) are indicated by one to three asterisks for *P*-values below 0.05, 0.01 and 0.001, respectively

mating propensity (Mt), refractory period between matings (MLt), spermatophore size (MSm), fighting ability (Mfa) and male calling duration (MCd). As predicted by the condition dependence hypothesis, there were positive correlations between some of these male traits, and no evidence of any negative correlations (the negative correlation between development time and spermatophore size is positive in relation to fitness effects). Combining data from males and females we found 12 significant correlations between traits, of which 11 were positive and one was negative. It is difficult to interpret our non-significant correlations, because the power of our sample size means that there may be correlations that we were unable to detect.

Our measure of Mfa is likely to be very closely allied to the measure of male mating success we used in our earlier study examining heritability of this trait (Wedell and Tregenza 1999). In that earlier study, two males were placed in a small enclosure with a female, a scenario which typically resulted in a fight between the males with the loser being prevented from accessing the female. Our measure of Mfa in the present study lacked detectable additive genetic variation, suggesting that it could not be involved in a negative trade-off with development time as had been observed previously (Wedell and Tregenza 1999). This difference may represent a difference between the populations of crickets used in the two studies, or it may represent a subtle distinction between competitive ability as measured in a fight and according to which of two males gains a mating, with the latter potentially including a significant element of female choice. Our study is also in contrast to previous work which found significant heritabilities for body size in this species (Simmons 1987b), although that study used parent-offspring regression and all offspring for a pair were reared together in a single box, creating the potential for large environmental effects.

The concept of condition dependence has been developed around the idea that fitness related traits require investment and hence that the overall pool of resources available to an individual must be divided up between them (see Tomkins et al. 2004 for review). The key prediction of the theory in relation to sexual selection is that male traits used by females in mate choice should be particularly condition dependent (Rowe and Houle 1996) and phenotypically correlated with one another. If they are not, any single trait cannot provide accurate information about an individual's condition. It is also instructive to examine the general pattern of phenotypic correlations between condition dependent traits because it is not clear whether we should expect to see a general pattern of positive correlations between all condition dependent traits or whether individuals can trade them off against one another. The key

sexually selected traits (Simmons 1986, 1987a, c, 1988a, b; Wedell and Tregenza 1999) we examined (Tables 3, 4) were the male traits of fighting ability, duration of calling song, how rapidly a spermatophore could be produced, how large the spermatophore was, how long a male took before mating, and how long he needed to wait between matings. We also examined development time and lifespan, which are not related to sexual selection. Because all these traits are closely related to fitness and inevitably under directional selection we can assume that they are condition dependent. As required by the condition dependence hypothesis, all significant correlations (and all those of $r \geq 0.1$) between male sexually selected traits were positive. This finding supports the condition dependent signalling hypothesis, although further experimental studies are required in which resources are manipulated such as that by Gray and Eckhardt (2001). Our study used individuals collected from the wild and utilised a very closely controlled laboratory rearing regime which minimised environmental variance by keeping individuals in a very simple environment. The low levels of additive genetic variance we found suggest that previous estimates using full-sib designs may have overestimated additive genetic variation, and point to the likely importance of non-additive variation in the substantial phenotypic variation in this species.

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References

Adamo SA, Hoy RR (1994) Mating-behavior of the field cricket *Gryllus bimaculatus* and its dependence on social and environmental cues. Anim Behav 47:857–868

Adamo SA, Hoy RR (1995) Agonistic behaviour in male and female field crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression. Anim Behav 49:1491–1501

Ashworth JR, Wall R (1994) Responses of the sheep blowflies *Lucilia sericata* and *L. cuprina* to odor and the development of semiochemical baits. Med Vet Entom 8:303–309

Bateman PW (1998) Mate preference for novel partners in the cricket *Gryllus bimaculatus*. Ecol Ent 23:473–475

Bateman PW, Gilson LN, Ferguson JWH (2001) Male size and sequential mate preference in the cricket *Gryllus bimaculatus*. Anim Behav 61:631–637

Bégin M, Roff DA (2002) The common quantitative genetic basis of wing morphology and diapause occurrence in the cricket *Gryllus veletis*. Heredity 89:473–479

Bretman A, Rodríguez-Muñoz R, Tregenza T (2006) Male dominance determines female egg laying rate in crickets. Biol Lett 2:409–411

Bretman A, Tregenza T (2005) Measuring polyandry in wild populations: a case study using promiscuous crickets. Mol Ecol 14:2169–2179

Bretman A, Wedell N, Tregenza T (2004) Molecular evidence of post-copulatory inbreeding avoidance in the field cricket *Gryllus bimaculatus*. Proc R Soc Lond B 271:159–164

Chen PS, Stummzollinger E, Aigaki T et al (1988) A male accessory gland peptide that regulates reproductive behavior of female *Drosophila melanogaster*. Cell 54:291–298

Christe P, Møller AP, Saino N et al (2000) Genetic and environmental components of phenotypic variation in immune response and body size of a colonial bird, *Delichon urbica* (the house martin). Heredity 85:75–83

Crnokrak P, Roff DA (1995) Dominance variance—associations with selection and fitness. Heredity 75:530–540

Czesak ME, Fox CW (2003) Genetic variation in male effects on female reproduction and the genetic covariance between the sexes. Evolution 57:1359–1366

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

Gray DA, Eckhardt G (2001) Is cricket courtship song condition dependent? Anim Behav 62:871–877

Grill CP, Moore AJ, Brodie ED (1997) The genetics of phenotypic plasticity in a colonizing population of the ladybird beetle, *Harmonia axyridis*. Heredity 78:261–269

Heifetz Y, Lung O, Frongillo EA et al (2000) The *Drosophila* seminal fluid protein Acp26Aa stimulates release of oocytes by the ovary. Curr Biol 10:99–102

Herndon LA, Chapman T, Kalb JM et al (1997) Mating and hormonal triggers regulate accessory gland gene expression in male drosophila. J Insect Physiol 43:1117–1123

Houle D (1992) Comparing evolvability and variability of quantitative traits. Genetics 130:195–204

Khazraïe K, Campan M (1999) The role of prior agonistic experience in dominance relationships in male crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae). Behav Process 44:341–348

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

Merila J, Sheldon BC (1999) Genetic architecture of fitness and nonfitness traits: empirical patterns and development of ideas. Heredity 83:103–109

Mezey JG, Houle D (2005) The dimensionality of genetic variation for wing shape in *Drosophila melanogaster*. Evolution 59:1027–1038

Morrow EH, Gage MJG (2001) Artificial selection and heritability of sperm length in *Gryllus bimaculatus*. Heredity 87:356–362

Pomiankowski A, Møller AP (1995) A resolution of the lek paradox. Proc R Soc Lond B 260:21–29

Réale D, Roff DA (2002) Quantitative genetics of oviposition behaviour and interactions among oviposition traits in the sand cricket. Anim Behav 64:397–406

Rowe L, Houle D (1996) The lek paradox and the capture of genetic variance by condition dependent traits. Proc R Soc Lond B 263:1415–1421

Sakai M, Taoda Y, Mori K et al (1991) Copulation sequence and mating termination in the male cricket gryllus-bimaculatus degeer. J Insect Physiol 37:599–615

Simmons LW (1986) Intermale competition and mating success in the field cricket, *Gryllus bimaculatus* (de Geer). Anim Behav 34:567–579

Simmons LW (1987a) Female choice contributes to offspring fitness in the field cricket *Gryllus bimaculatus* (de Geer). Behav Ecol Sociobiol 21:313–321

Simmons LW (1987b) Heritability of a male character chosen by females of the field cricket, *Gryllus bimaculatus*. Behav Ecol Sociobiol 21:129–133

Simmons LW (1987c) Sperm competition as a mechanism of female choice in the field cricket, *Gryllus bimaculatus*. Behav Ecol Sociobiol 21:197–202

Simmons LW (1988a) The contribution of multiple mating and spermatophore consumption to the lifetime reproductive success of female field crickets (*Gryllus bimaculatus*). Ecol Ent 13:57–69

Simmons LW (1988b) Male size, mating potential and lifetime reproductive success in the field cricket, *Gryllus bimaculatus* (de Geer). Anim Behav 36:372–379

Simons AM, Roff DA (1994) The effect of environmental variability on the heritabilities of traits of a field cricket. Evolution 48:1637–1649

Tachon G, Murray AM, Gray DA et al (1999) Agonistic displays and the benefits of fighting in the field cricket, *Gryllus bimaculatus*. J Insect Behav 12:533–543

Tomkins JL, Radwan J, Kotiaho JS et al (2004) Genic capture and resolving the lek paradox. Trends Ecol Evol 19:323–328

Tregenza T, Wedell N (1997) Definitive evidence for cuticular pheromones in a cricket. Anim Behav 54:979–984

Tregenza T, Wedell N (1998) Benefits of multiple mates in the cricket *Gryllus bimaculatus*. Evolution 52:1726–1730

Tregenza T, Wedell N (2000) Genetic compatibility, mate choice and patterns of parentage. Mol Ecol 9:1013–1027

Tregenza T, Wedell N (2002) Polyandrous females avoid costs of inbreeding. Nature 415:71–73

Wade MJ (2002) A gene's eye view of epistasis, selection and speciation. J Evol Biol 15:337–346

Wedell N, Tregenza T (1999) Successful fathers sire successful sons. Evolution 53:620–625