Evolutionary Ecology Research, 2010, **12**: 389–402

Female social experience affects the shape of sexual selection on males

Kevin A. Judge

Department of Biology, University of Toronto Mississauga, Mississauga, Ontario, Canada

ABSTRACT

Background: An increasing number of factors have been shown to affect female mating behaviour, and thus to affect the strength and/or direction of selection that females exert on males. One of these factors is female social experience (including mating history).

Question: How does female social experience affect the strength and direction of selection on four male traits – age, body size, weaponry size, and body condition?

Methods: I used multivariate selection analysis to estimate the linear and non-linear selection gradients exerted by female field crickets (*Gryllus pennsylvanicus*) with different social backgrounds. Females were either virgins with no experience of conspecifics as adults or experienced females from a large, mixed-sex population. I assessed relative fitness through mating success (mated or not) and calculated selection gradients for the four male traits.

Results: Experienced females exerted significant positive directional selection on male weaponry size and favoured older males. However, linear variation in these traits did not affect the probability of an inexperienced female mating. I also detected correlational selection by inexperienced females, who preferred combinations of age and body size (old/large and young/small).

Keywords: *Gryllus pennsylvanicus*, head size, male age, mate choice, no-choice trials, selection analysis.

INTRODUCTION

Female mating behaviour is affected by a variety of factors, including parasite infection (e.g. Morris *et al.*, 1975), predation risk (e.g. Hedrick and Dill, 1993), age (e.g. Gray, 1999), condition (e.g. Hunt *et al.*, 2005), ambient light spectrum (e.g. Gamble *et al.*, 2003), ambient acoustic environment (e.g. Gerhardt and Klump, 1988), and juvenile experience (e.g. Hebets, 2003) among many others (reviewed in Jennions and Petrie, 1997). However, these effects on mating behaviour are usually documented as simple effects on, for example: (a) female receptivity to mating in general (e.g. Leopold *et al.*, 1971, and references therein; Lickman *et al.*, 1998), (b) the time/effort spent choosing a mate (e.g. Milinski and Bakker, 1992; Hunt *et al.*, 2005) or (c) the choice of which male to mate with (e.g. Hedrick and Dill, 1993) (for an

---

Correspondence: K.A. Judge, Department of Biological Sciences, University of Lethbridge, Lethbridge, Alberta T1K 3M4, Canada. e-mail: kevin.judge@uleth.ca

extensive review, see Jennions and Petrie, 1997). All of these (and other) female responses have the potential to affect the strength and shape of selection on male phenotype. However, given that selection is a complex, multivariate process (Brooks *et al.*, 2005; Bentsen *et al.*, 2006), surprisingly few studies have examined the ultimate effects of variation in female mating behaviour on multivariate phenotypic selection (but see below for exceptions).

Variation in female mating behaviour may affect both the strength and the shape of selection on males (Jennions and Petrie, 1997). The strength of selection may change if, for example, females in poor condition are more likely to mate with any male (e.g. Poulin, 1994; Simmons, 1994), thus weakening selection. Or they may be less likely to mate (e.g. Ortigosa and Rowe, 2002), potentially making selection stronger if: (a) successful males are an extreme subset of males who are already attractive, and (b) mating with a female in poor condition is not costly. Alternatively, females may not change their receptivity to mating, but instead change their choice of mate (e.g. Hedrick and Dill, 1993), thus changing the shape of selection on males. By simply examining variation in female mating behaviour from the perspective of summary measures of selection such as the probability of mating or latency to mate, or from the perspective of simple univariate choices (e.g. between large and small males), researchers may be missing important changes in multivariate selection (e.g. different traits or combinations of traits may be important to different females). Thus it is critical to our understanding of the evolution of female preferences and male phenotype to take a multivariate approach (Lande and Arnold, 1983; Phillips and Arnold, 1989) to measuring the effects of changes in female behaviour on selection on males.

Two recent studies have taken such a multivariate approach. In the house cricket, *Acheta domesticus*, large daughters of attractive males preferred large males, whereas all daughters of unattractive males preferred intermediate-sized males (Head *et al.*, 2006). Hall *et al.* (2008) found that when male *Teleogryllus commodus* were prevented from mate guarding, their mates exerted multivariate stabilizing selection, but when males were present, selection exerted by females was multi-modal. In this paper, I quantify net selection, and both linear and non-linear selection exerted on multiple male traits by female fall field crickets *Gryllus pennsylvanicus* (Burmeister) with two different backgrounds: (1) virgin females that had no experience as adults of conspecifics of either sex, and (2) experienced females from a large, mixed-sex population, thus experienced in conspecific interactions including mating.

Gryllus pennsylvanicus is a common, univoltine species found in grassy, disturbed areas (Alexander, 1968; personal observation) across North America (Capinera *et al.*, 2004). Eggs hatch in the spring and adults mate by mid-July. Breeding continues throughout the fall – hence the common name – until the first severe frost (Alexander, 1968). Female *G. pennsylvanicus* have a mating bias for older males (Zuk, 1987a, 1988), although this may be because males in good condition both live longer and call more than males in poor condition (Judge *et al.*, 2008). Male gryllines use their heads and mouthparts during violent male–male combat (Alexander, 1961), and male *G. pennsylvanicus* have larger heads and more widely spaced maxillae (pointed, sclerotized mouthparts used in male–male fights) than females for a given body size (Judge and Bonanno, 2008). Moreover, male *G. pennsylvanicus* with more widely spaced maxillae are more likely to win in aggressive contests with males with less widely spaced maxillae (Judge and Bonanno, 2008).

I measured selection on male age (days past adult moult), body size (pronotum length), relative head size (residual head width), and condition (residual body mass). I predicted that there would be positive linear selection on all four male characteristics because females show a mating bias towards older males (Zuk, 1987a, 1988), and males in good condition invest more in calling effort (Judge *et al.*, 2008), are larger and have proportionately wider heads (K.A. Judge, unpublished data) than males in poor condition. Furthermore, because experienced females have likely mated and definitely experienced a wider variance in mate quality than inexperienced females, experienced females should exert stronger selection than inexperienced females [mating (e.g. Gabor and Halliday, 1997), variance in mate quality (e.g. Wagner *et al.*, 2001)]. However, experienced females may be older and in poorer condition than inexperienced females, characteristics that would tend to lessen the choosiness of experienced females [age (e.g. Gray, 1999), condition (e.g. Hunt *et al.*, 2005)].

METHODS

Animal rearing

All experimental individuals were first-generation offspring of approximately 150 male and 150 female adult *G. pennsylvanicus* collected from around the campus of the University of Toronto Mississauga campus (43°32′50.51″N, 79°39′37.80″W) in August and September 2004.

Juveniles were held in large plastic bins (48 cm long, 35 cm wide, 31 cm high). I fed all juvenile crickets rabbit chow (Little Friends Rabbit Food, Martin Mills, Inc., ground pellets for the first 2–3 weeks after hatching and whole pellets after). Water was provided in cotton-plugged plastic vials, and shelter consisted of layers of egg cartons. New food was added and water vials changed as needed every 3–4 days. To reduce cannibalism of smaller individuals, I moved mid- to late-instar nymphs to a separate bin. I isolated penultimate-instar nymphs in individual containers (9 cm in diameter, 8 cm high) with two pieces of food, a cotton-plugged water vial, and a small piece of egg carton. Food in individual containers was changed weekly and water was changed at least fortnightly or more frequently if needed.

Experienced females were from a large mixed-sex bin of adults with access to food and water *ad libitum* (approximately 150 males and 150 females) in which individuals likely acquired at least one mating, and were individually isolated at least 24 h before the experiment. Both inexperienced females and males were housed individually from the last nymphal instar (see above) and so had no adult experience of conspecifics. Inexperienced and experienced females differ in a variety of ways that could affect their mating behaviour, such as mating status, age, and experience with conspecifics. I discuss the likely causal factors in the Discussion.

Morphological measurements

On the day following his moult to adulthood, each male was weighed using a Mettler AE 50 balance to the nearest milligram. To measure head width and pronotum length (using NIH Image 1.62), I restrained crickets on the surface of a petri dish with a small piece of plastic wrap weighed down by a plastic ring. This allowed me to position the cricket so that the frontal plane was perpendicular to the line of sight under a dissecting microscope, which had a camera mounted on it to transmit live images to a computer. Focal height of the microscope was fixed for each measurement, which ensured a high degree of repeatability for each of these measurements ($r_{\mathrm{(head\ width)}} = 99.4\%$, $r_{\mathrm{(pronotum\ length)}} = 99.1\%$).

Mating trials

Each male ($n = 94$) was paired with an inexperienced female and an experienced female on consecutive days. The average age of males on day 1 of the experiment was 16.8 days (S.D. = 5.9) post adult moult and ranged from 7 to 31 days, which matches the natural range of male ages found in wild populations (Zuk, 1987b; Murray and Cade, 1995). Inexperienced females were all at least 10 days post adult molt and thus sexually mature (personal observation), and although experienced females were of unknown age most were likely older than 10 days post adult moult. I randomly assigned the order in which each male encountered the two classes of female, so that half of the males encountered the inexperienced female on day 1 and the other half on day 2. For each mating trial, I moved males and females to clean containers; the female's container had a paper towel circle for substrate. Approximately 2 min later, I introduced the male into the female's container. I recorded the time until the male initiated courtship (latency to court, to the nearest minute) and the time from courtship initiation until copulation (latency to copulate, to the nearest second). If a male failed to initiate courtship within 30 min, I separated the pair and attempted the mating trial again at the end of the day with a new female. If the male did not court the new female, he was discarded. After the male initiated courtship, I scored him as successful if the female started copulating within 20 min, and unsuccessful if she did not. I used a 20-min threshold because in a separate experiment, 95% of females chose a speaker within 20 min in two-speaker phonotaxis trials (K.A. Judge *et al.*, in preparation). After 20 min, the pair was separated and both insects placed back in their original individual containers. Each female was used only once.

Statistical analyses

I determined four traits for each male for inclusion in the selection analysis: adult age (days past adult moult), body size (pronotum length), residual head width, and residual mass. Residual head width and residual mass were the y-axis residuals from two separate linear regressions: of head width on pronotum length and of mass on pronotum length respectively. Residual head width is sexually dimorphic in this species, with males having a wider head than females for a given body size (Judge and Bonanno, 2008). Residual mass is an index of condition and is hypothesized to represent energy reserves (Jakob *et al.*, 1996; Schulte-Hostedde *et al.*, 2005). I standardized each trait to a mean of zero and standard deviation of one for all selection analyses.

I calculated selection differentials, univariate linear selection gradients, univariate non-linear selection gradients, and bivariate non-linear selection gradients (Lande and Arnold, 1983) on age, body size, residual head width, and residual mass. Selection differentials estimate net (both direct and indirect) linear selection on the trait of interest, whereas univariate selection gradients estimate direct linear selection. Univariate non-linear selection gradients estimate the shape of selection (concave up or concave down) on a trait, and bivariate non-linear selection gradients estimate selection on combinations of traits (i.e. correlational selection) (Lande and Arnold, 1983; Phillips and Arnold, 1989). I estimated selection coefficients for selection exerted by inexperienced and experienced females separately using mating success (mated or not mated) as the measure of fitness. All selection coefficients were estimated using ordinary least squares regression in the following ways: (1) selection differentials were the regression coefficients of univariate regressions of fitness on each individual trait; (2) univariate selection gradients were given by the partial regression coefficients from a multiple linear regression of fitness on all four traits; and (3) univariate and bivariate non-linear gradients were given by the partial regression coefficients from a multiple regression of fitness on all four traits, all four traits squared, and all possible cross-products between traits. The quadratic coefficients given by the statistical package were doubled to give the appropriate univariate non-linear selection gradients (Stinchcombe *et al.*, 2008). I used permutation tests (Legendre and Legendre, 1998) carried out using PopTools (Hood, 2009) to test the statistical significance of selection coefficients. To further examine non-linear selection, I also conducted canonical rotation (Philips and Arnold, 1989; Blows and Brooks, 2003) of the matrices of non-linear selection gradients for both inexperienced and experienced females using PopTools (Hood, 2009).

To compare selection exerted by inexperienced females to selection exerted by experienced females, I conducted a repeated-measures general linear model with female experience (inexperienced vs. experienced) as the within-subjects factor and the four male traits both (1) alone (for comparisons of the linear gradients) and (2) together with the squared and cross-product terms (for comparisons of the non-linear gradients) as between-subjects covariates; the dependent variable was relative fitness. I interpret a significant interaction between female experience and any of the covariates as an indication that inexperienced and experienced females differ in the selection gradient that they exert on males.

To investigate the possibility that males might adjust their courtship based on the class of female they encounter, I analysed males' latency to court using a repeated-measures general linear model with female experience as the within-subjects factor and female order (inexperienced female first or experienced female first) as the between-subjects factor; the dependent variable was latency to court. I interpret a significant interaction between female experience and female order as indicating male choice behaviour, particularly if all males courted the first female equally and there was a drop in males' willingness to court the second female depending on her background.

All statistical analyses, except permutation tests and canonical rotations, were carried out using SPSS 10 for Windows (SPSS, Inc.). All tests were two-tailed and carried out with an *a priori* Type I error rate of 5%.

Visualization of selection

To visualize multivariate fitness surfaces, I used thin-plate splines, which were estimated using the Tsp function in the *fields* package of R (available at: http://www.r-project.org). Splines were fitted that used a value of the smoothing parameter (λ) that minimized the generalized cross-validation (GCV) score.

RESULTS

All four male traits were normally distributed and for the most part phenotypically uncorrelated with one another (Table 1). The exceptions to this were residual head width and residual mass, which were strongly positively intercorrelated ($r = 0.626$, $P < 0.001$; Table 1).

Seventeen of the 94 males failed to court the inexperienced female (five males), the experienced female (four males) or both (eight males), and were removed from all subsequent analyses. Experienced females were significantly more likely to reject males as mates (33/77 = 42.9%) than inexperienced females (10/77 = 13.0%; $\chi^2 = 17.07$, $P < 0.001$).

Table 1. Phenotypic correlations between the four male traits in the initial sample of male field crickets

Trait	*n*	Mean	s.d.	PL	RM	AGE
Residual head width, RHW (mm)	94	0.000	0.176	0.000	0.612*	0.063
Pronotum length, PL (mm)	94	2.953	0.268		0.000	−0.007
Residual mass, RM (mm)	94	0.000	0.037			0.034
Mean age, AGE (days)	94	17.330	5.931			

* $P < 0.001$.

Table 2. Standardized linear selection differentials (s), linear selection gradients (β), and the matrix of non-linear selection gradients (γ) exerted on four male characters by females of two different experience classes (inexperienced or experienced)

Class of female			γ			
Male character	s	β	RHW	PL	RM	AGE
Inexperienced females						
RHW	0.016	0.028	0.015			
PL	0.057	0.054	0.025	−0.052		
RM	−0.006	−0.020	0.049	−0.037	−0.121	
AGE	−0.046	−0.046	−0.109[#]	**0.121**	0.071	−0.037
Experienced females						
RHW	0.150	**0.271**	−0.032			
PL	−0.096	−0.115	0.120	0.198		
RM	−0.015	−0.188	0.120	0.167	−0.511[#]	
AGE	**0.210**	**0.206**	−0.017	−0.021	0.079	0.152

Note: Abbreviations for male characters are as follows: RHW = residual head width; PL = pronotum length; RM = residual mass; AGE = mean age. **Bold** values are statistically significant at $P < 0.05$.

[#] $P < 0.10$.

Selection on male traits

There was less opportunity for sexual selection [I = variance in relative fitness (Arnold and Wade, 1984)] on males exerted through mating success with inexperienced females than with experienced females [$I_{\mathrm{inexperienced}} = 0.151$ and $I_{\mathrm{experienced}} = 0.760$; variance ratio test (Zar, 1996): $F_{76,76} = 5.03$, $P < 0.001$].

I detected no significant net selection on male traits exerted through inexperienced females (s = standardized selection differential: all $|s| < 0.058$, all $P > 0.203$; Table 2). However, experienced females favoured older males over younger males ($s = 0.210$, $P = 0.034$), but exerted no net selection on any other male traits (all $|s| < 0.151$, all $P > 0.134$; Table 2). Only the selection differentials for age differed significantly between inexperienced and experienced females (repeated-measures ANOVA: $F_{1,75} = 6.088$, $P = 0.016$; all other $P > 0.155$).

No significant linear selection by inexperienced females was detected (β = standardized linear selection gradient: all $|\beta| < 0.055$, all $P > 0.232$; Table 2). However, experienced females exerted positive linear selection on residual head width ($\beta = 0.271$, $P = 0.031$) and favoured older males ($\beta = 0.206$, $P = 0.035$) (Table 2). There was negative linear selection on body size and residual mass in the experienced female treatment, although neither of these two selection gradients was statistically significant (Table 2). Inexperienced and experienced females differed in the linear relationship between fitness and male age (repeated-measures ANOVA: female experience × age: $F_{1,72} = 6.085$, $P = 0.016$; Fig. 1), but not residual head width ($F_{1,72} = 3.432$, $P = 0.068$).

In contrast to the linear selection gradients, I detected significant non-linear selection on males by inexperienced females (Table 2). There was significant positive correlational selection between male body size and age ($\gamma = 0.121$, $P = 0.014$; Table 2) indicating that larger/older and smaller/younger males were selected, whereas other combinations of these two traits were not. One non-linear selection gradient for the experienced females was marginally non-significant: the quadratic gradient for male residual mass ($\gamma = -0.511$, $P = 0.054$; Table 2). Inexperienced and experienced females did not differ in any of the non-linear gradients that they exerted on males (repeated-measures ANOVA: all $P > 0.160$).

Canonical rotation of the matrix of non-linear selection gradients (γ) exerted by inexperienced females revealed one statistically significant vector of positive non-linear selection (m_1, Table 3). Residual head width and age loaded heavily (i.e. > 0.5) on m_1, indicating that selection was acting in a disruptive manner: large headed/younger and small headed/older individuals were favoured but not intermediate individuals. There was one statistically significant vector of positive linear selection exerted by experienced females (m_3, Table 3). Residual head width was the only trait that loaded strongly on vector m_3 – selection favoured males with bigger residual head widths. Because canonical rotation must be done on the gamma matrices for inexperienced and experienced females separately, the resulting

Table 3. *M* matrices of eigenvectors (m_i) from the canonical rotation of the γ matrices in Table 2

Class of female	M				Selection	
m_i	RHW	PL	RM	AGE	θ_i	λ_i
Inexperienced females						
m_1	0.595	−0.390	−0.027	−0.702	0.028	**0.125**
m_2	0.711	0.617	0.223	0.252	0.038	0.013
m_3	0.068	−0.495	0.813	0.301	−0.055	−0.068
m_4	−0.368	0.472	0.538	−0.594	0.032	−0.265
Experienced females						
m_1	0.407	0.881	0.237	−0.042	−0.117	0.299#
m_2	−0.001	0.015	0.120	0.993	0.486#	0.161
m_3	0.896	−0.436	0.081	−0.002	**0.737**	−0.079
m_4	−0.176	−0.183	0.961	−0.114	−0.590#	−0.574#

Note: Linear and quadratic selection gradients along each eigenvector are given by θ_i and λ_i respectively. Abbreviations for male characters are as follows: RHW = residual head width; PL = pronotum length; RM = residual mass; AGE = mean age. **Bold** values are statistically significant at $P < 0.05$.

# $P < 0.10$

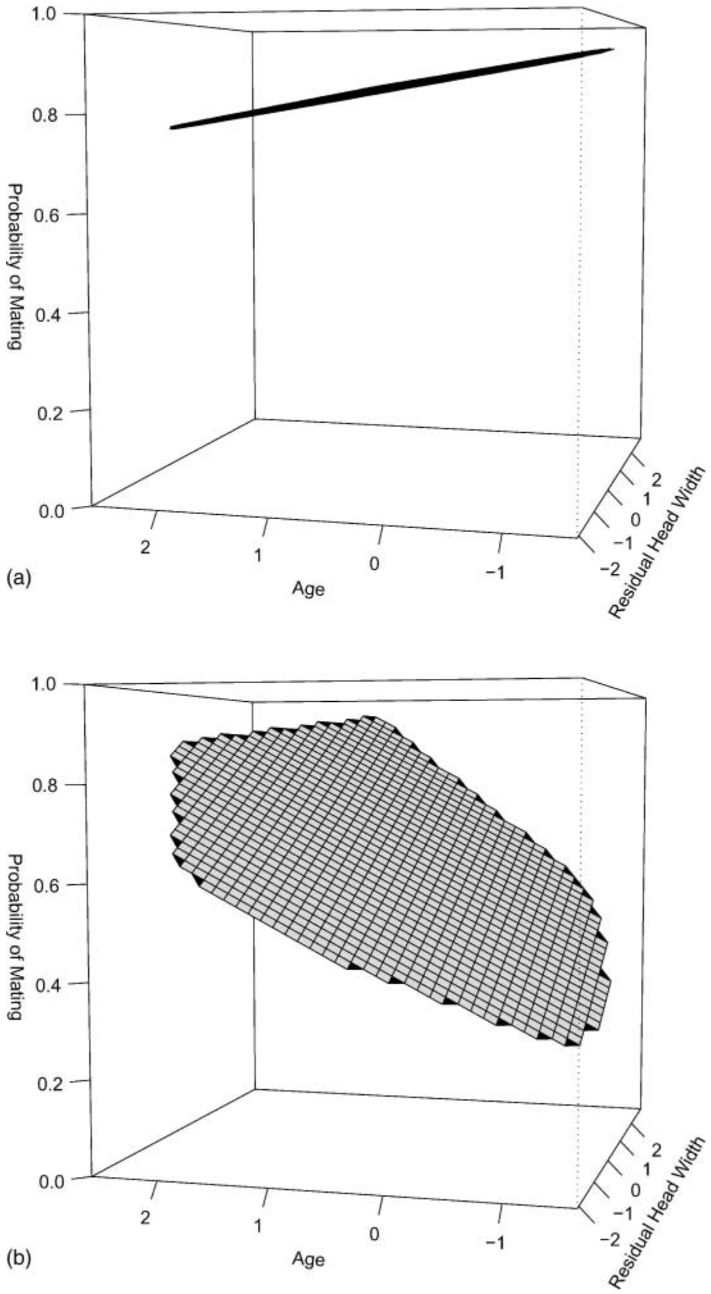

Fig. 1. Thin-plate splines representing selection exerted by (a) inexperienced females and (b) experienced females on male age and residual head width.

multivariate axes are not statistically comparable. For comparison's sake, I present visualizations of fitness along both the statistically significant axis of selection and the axis of next largest magnitude, for both inexperienced and experienced females (Figs. 2 and 3, respectively).

Latency to court

There was no significant female experience × order interaction (repeated-measures ANOVA: $F_{1,75} = 0.015$, $P = 0.904$), indicating that males' latency to court either inexperienced or experienced females did not depend on the order in which they were encountered. However, there was a significant effect of female experience ($F_{1,75} = 6.953$, $P = 0.010$): males took significantly longer to court experienced females than inexperienced females [mean ± s.e. difference in latency to court (experienced – inexperienced): 1.18 ± 0.45 min].

DISCUSSION

In general, the results of this study show that inexperienced female field crickets were less choosy than experienced females, and that experienced females favoured older over younger males (Table 2). Also, I found that inexperienced and experienced females differed in the form of selection (i.e. linear or non-linear) that they exerted on males: experienced females exerted linear selection whereas inexperienced females exerted only non-linear selection on males (Tables 2 and 3). Comparison of the linear and non-linear selection gradients exerted

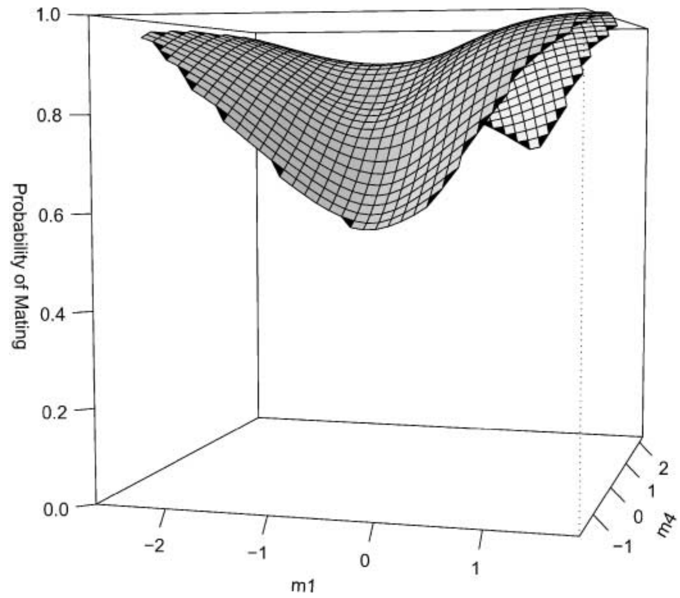

Fig. 2. Thin-plate spline representing selection exerted by inexperienced females along two multivariate axes, m_1 (trait loadings: 0.595RHW, −0.390PL, −0.027RM, −0.702AGE) and m_4 (−0.368RHW, 0.472PL, 0.538RM, −0.594AGE). There was statistically significant non-linear selection along m_1 only. RHW = residual head width; PL = pronotum length; RM = residual mass; AGE = mean age.

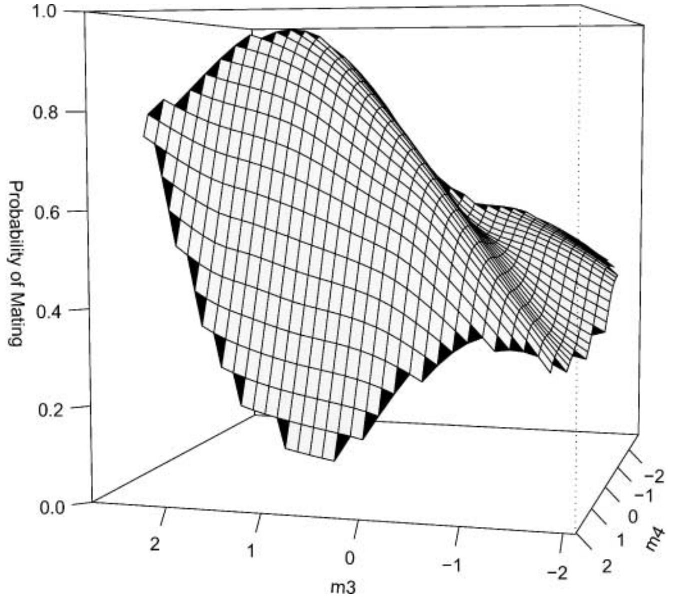

Fig. 3. Thin-plate spline representing selection exerted by experienced females along two multivariate axes, m_3 (trait loadings: 0.896RHW, −0.436PL, 0.081RM, −0.002AGE) and m_4 (−0.176RHW, −0.183PL, 0.961RM, −0.114AGE). There was statistically significant linear selection along m_3 only. RHW = residual head width; PL = pronotum length; RM = residual mass; AGE = mean age.

by the different classes of female revealed significant differences in the direction and shape of selection exerted on males. Experienced females appeared to select males that were older (Table 2; Fig. 1b) and had relatively larger heads (Table 2), whereas inexperienced females tended to select combinations of male traits (correlational selection); for example, smaller/younger or larger/older males were favoured.

Although other studies have compared the choosiness of females differing in some characteristic such as parasitism status (e.g. Poulin, 1994; Simmons, 1994) or population of origin (e.g. Gwynne, 1984), this is only the third study to find that the shape of sexual selection differed between two classes of females. The first was by Head *et al.* (2006), who compared the selection on males exerted by daughters of attractive fathers in *Acheta domesticus* to that exerted by daughters of unattractive fathers. They found that the large daughters of attractive males mated preferentially with the largest males, whereas all daughters of unattractive males mated preferentially with intermediate-sized males (Head *et al.*, 2006). In the second study, Hall *et al.* (2008) found that selection exerted by female *Teleogryllus commodus* held with males after copulation was primarily disruptive, whereas when they were held alone it was stabilizing. In the current study, experienced female *G. pennsylvanicus* exerted strong linear selection on males, whereas inexperienced females exerted weak non-linear selection. This non-linear selection by inexperienced females would have been missed by a simple univariate approach to female preferences, and one would have concluded that inexperienced females were completely unselective instead of selecting combinations of male traits. Further work is required to determine what the selective advantage to inexperienced females is of mating with smaller/younger or larger/older males.

Previous work on *G. pennsylvanicus* found that older males had a mating advantage over younger males (Zuk, 1987a, 1988). In a field enclosure experiment, the number of laboratory-reared virgin females that a male attracted was significantly positively related to his age. This finding was supported when males of two age classes (old: > 14 days; young: 7–9 days) were placed in an open field and allowed to attract wild females: older males attracted more wild females than younger males (Zuk, 1987a). In another study, Zuk (1988) found that wild males taken paired with a female in the field were significantly older than a wild, unpaired singing male from close by. In the present study, older males were more likely than younger males to mate with experienced females (Table 3). In light of the many differences (i.e. experimental methods, population of origin, time period) between our two studies, the common finding that male age (or some correlate thereof) is under significant positive selection in *G. pennsylvanicus* takes on added significance (Kelly, 2006). There is weak evidence to suggest that male age is signalled directly through his calling song (Ciceran *et al.*, 1994; K.A. Judge, in preparation), making selection on male age *per se* unlikely. However, recent work on the condition dependence of male lifespan and calling effort found that males of high condition both lived longer and called more than males of low condition (Judge *et al.*, 2008). Thus, female selection for 'older' males may in fact represent selection for males in good condition and/or males who invest more in calling effort. I was unable to measure males' calling effort in this study, so I am unable to directly evaluate this hypothesis. However, subsequent research has shown that females are attracted to greater investment in calling effort (K.A. Judge *et al.*, in preparation).

Males initiated courtship faster with inexperienced females than with experienced females, but latency to court did not depend on the order in which males encountered the inexperienced and experienced females. The question arises whether this is male mate choice behaviour, or a consequence of differences in the behaviour of inexperienced and experienced females. Males of many insect species display a preference for virgin over mated females (reviewed in Bonduriansky, 2001), and the relatively greater alacrity with which males of *G. pennsylvanicus* courted inexperienced females (who were all virgin) may represent a male preference for reduced risk of sperm competition. An interaction between female experience and female order on latency to court might indicate male choice behaviour, especially if all males courted the first female equally and there was a drop in males' willingness to court the second female if she was an experienced female; however, this was not the case. The alternative hypothesis to male mate choice is that experienced females behaved in such a way as to inhibit males from initiating courtship. This seemed to be the case, as experienced females appeared much more active while in the mating arena, walking into and over courting males, disrupting their courtship singing (personal observation). Further research is needed to distinguish between alternative hypotheses for the apparent trend of males to court inexperienced females more rapidly than experienced females.

The results of the current study provide support for the prediction (Bateman, 1948) that virgin females should be less reluctant to mate than mated females (e.g. Gabor and Halliday, 1997; Bateman *et al.*, 2001; Ortigosa and Rowe, 2003; Pitcher *et al.*, 2003; Uetz and Norton, 2007; but see Ivy *et al.*, 2005, for a contrary example). All of the inexperienced females in my study were virgins and most, if not all, of the experienced females had mated at least once. Although I did not directly manipulate the mating history of the experienced females used in this experiment, the expected variation in these females' mating history should have introduced variation to the results and made selection differentials and gradients harder to detect. Experienced females were also likely to be older than the inexperienced females, although mating status has been shown to have a much greater effect on female choosiness in this species than female age (Judge *et al.*, 2010).

Another factor that could explain the difference in selection exerted by inexperienced and experienced females is their housing conditions. Inexperienced females were housed in isolation from the time they were late-instar nymphs, whereas experienced females were removed from a large breeding colony a minimum of only 24 h before the experiment. This difference in female experience of both the number of potential mates as well as the distribution of mate quality could have caused the differences in selection that I detected. Female crickets are known to adjust their preferences based on the variation in male quality that they encounter (Wagner *et al.*, 2001), and reduced exposure to male song in the juvenile phase made female *T. oceanicus* females much less selective when they were adults (Bailey and Zuk, 2008). Coupled with the present study, these results highlight the plastic nature of sexual selection, a fact that is now getting much deserved attention (for a recent review, see Cornwallis and Uller, 2010). Future researchers could manipulate female *G. pennsylvanicus* experience of the number and variation in quality of potential male mates to assess the impact this form of social experience has on the shape and direction of female preferences.

ACKNOWLEDGEMENTS

Many thanks to Michelle den Hollander, Mark Fitzpatrick, and Kim-Chi Tran for their invaluable help with no-choice trials. David Punzalan was very generous with his time in discussions about selection analyses. Mark Fitzpatrick and Clint Kelly raised important issues with statistical analyses. Luc Bussière, Mark Fitzpatrick, Darryl Gwynne, John Hunt, Glenn Morris, David Punzalan, Locke Rowe, and two anonymous reviewers made helpful comments on earlier drafts of the manuscript. Special thanks to Darryl Gwynne for his constant support and encouragement to attempt to replicate earlier work on this species. This work was funded by an NSERC Postgraduate Scholarship to the author and an NSERC Discovery grant to Darryl Gwynne.

REFERENCES

Alexander, R.D. 1961. Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). *Behaviour*, **17**: 130–223.

Alexander, R.D. 1968. Life cycle origins, speciation, and related phenomena in crickets. *Quart. Rev. Biol.*, **43**: 1–41.

Arnold, S.J. and Wade, M.J. 1984. On the measurement of natural and sexual selection: theory. *Evolution*, **38**: 709–719.

Bailey, N.W. and Zuk, M. 2008. Acoustic experience shapes female mate choice in field crickets. *Proc. R. Soc. Lond. B*, **275**: 2645–2650.

Bateman, A.J. 1948. Intra-sexual selection in *Drosophila. Heredity*, **2**: 349–368.

Bateman, P.W., Gilson, L.N. and Ferguson, J.W.H. 2001. Male size and sequential mate preference in the cricket *Gryllus bimaculatus. Anim. Behav.*, **61**: 631–637.

Bentsen, C.L., Hunt, J., Jennions, M.D. and Brooks, R. 2006. Complex multivariate sexual selection on male acoustic signaling in a wild population of *Teleogryllus commodus. Am. Nat.*, **167**: E102–E116.

Blows, M.W. and Brooks, R. 2003. Measuring nonlinear selection. *Am. Nat.*, **162**: 815–820.

Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol. Rev.*, **76**: 305–339.

Brooks, R., Hunt, J., Blows, M.W., Smith, M.J., Bussière, L.F. and Jennions, M.D. 2005. Experimental evidence for multivariate stabilizing sexual selection. *Evolution*, **59**: 871–880.

Capinera, J.L., Scott, R.D. and Walker, T.J. 2004. *Field Guide to Grasshoppers, Katydids, and Crickets of the United States*. Ithaca, NY: Comstock Publishing.

Ciceran, M., Murray, A.-M. and Rowell, G. 1994. Natural variation in the temporal patterning of calling song structure in the field cricket *Gryllus pennsylvanicus*: effects of temperature, age, mass, time of day, and nearest neighbour. *Can. J. Zool.*, **72**: 38–42.

Cornwallis, C.K. and Uller, T. 2010. Towards an evolutionary ecology of sexual traits. *Trends Ecol. Evol.*, **25**: 145–152.

Gabor, C.R. and Halliday, T.R. 1997. Sequential mate choice by multiply mating smooth newts: females become more choosy. *Behav. Ecol.*, **8**: 162–166.

Gamble, S., Lindholm, A.K., Endler, J.A. and Brooks, R. 2003. Environmental variation and the maintenance of polymorphism: the effect of ambient light spectrum on mating behaviour and sexual selection in guppies. *Ecol. Lett.*, **6**: 463–472.

Gerhardt, H.C. and Klump, G.M. 1988. Masking of acoustic signals by the chorus background noise in the green tree frog: a limitation on mate choice. *Anim. Behav.*, **36**: 1247–1249.

Gray, D.A. 1999. Intrinsic factors affecting female choice in house crickets: time cost, female age, nutritional condition, body size, and size-relative reproductive investment. *J. Insect Behav.*, **12**: 691–700.

Gwynne, D.T. 1984. Sexual selection and sexual differences in mormon crickets (Orthoptera: Tettigoniidae, *Anabrus simplex*). *Evolution*, **38**: 1011–1022.

Hall, M.D., Bussière, L.F., Hunt, J. and Brooks, R. 2008. Experimental evidence that sexual conflict influences the opportunity, form and intensity of sexual selection. *Evolution*, **62**: 2305–2315.

Head, M.L., Hunt, J. and Brooks, R. 2006. Genetic association between male attractiveness and female differential allocation. *Biol. Lett.*, **2**: 341–344.

Hebets, E.A. 2003. Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. *Proc. Natl. Acad. Sci. USA*, **100**: 13390–13395.

Hedrick, A.V. and Dill, L.M. 1993. Mate choice by female crickets is influenced by predation risk. *Anim. Behav.*, **46**: 193–196.

Hood, G.M. 2009. *PopTools*, version 3.1.1 (available online at: http://www.cse.csiro.au/poptools).

Hunt, J., Brooks, R. and Jennions, M.D. 2005. Female mate choice as a condition-dependent life-history trait. *Am. Nat.*, **166**: 79–92.

Ivy, T.M., Weddle, C.B. and Sakaluk, S.K. 2005. Females use self-referent cues to avoid mating with previous mates. *Proc. R. Soc. Lond. B*, **272**: 2475–2478.

Jakob, E.M., Marshall, S.D. and Uetz, G.W. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*, **77**: 61–67.

Jennions, M.D. and Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.*, **72**: 283–327.

Judge, K.A. and Bonanno, V.L. 2008. Male weaponry in a fighting cricket. *PLoS ONE*, **3**: e3980.

Judge, K.A., Ting, J.J. and Gwynne, D.T. 2008. Condition dependence of male life span and calling effort in a field cricket. *Evolution*, **62**: 868–878.

Judge, K.A., Tran, K.-C. and Gwynne, D.T. 2010. The relative effects of mating status and age on the mating behaviour of female field crickets. *Can. J. Zool.*, **88**: 219–223.

Kelly, C.D. 2006. Replicating empirical research in behavioral ecology: how and why it should be done but rarely ever is. *Quart. Rev. Biol.*, **81**: 221–236.

Lande, R. and Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution*, **37**: 1210–1226.

Legendre, P. and Legendre, L. 1998. *Numerical Ecology* (second English edition). Amsterdam: Elsevier.

Leopold, R.A., Terranova, A.C. and Swilley, E.M. 1971. Mating refusal in *Musca domestica*: effects of repeated mating and decerebration upon frequency and duration of copulation. *J. Exp. Zool.*, **176**: 353–360.

Lickman, K., Murray, A.-M. and Cade, W.H. 1998. Effect of mating on female phonotactic response in *Gryllus integer* (Orthoptera: Gryllidae). *Can. J. Zool.*, **76**: 1263–1268.

Milinski, M. and Bakker, T.C.M. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus. Proc. R. Soc. Lond. B*, **250**: 229–233.

Morris, G.K., Kerr, G.E. and Gwynne, D.T. 1975. Ontogeny of phonotaxis in *Orchelimum gladiator* (Orthoptera: Tettigoniidae: Conocephalinae). *Can. J. Zool.*, **53**: 1127–1130.

Murray, A.-M. and Cade, W.H. 1995. Differences in age structure among field cricket populations (Orthoptera; Gryllidae): possible influence of a sex-biased parasitoid. *Can. J. Zool.*, **73**: 1207–1213.

Ortigosa, A. and Rowe, L. 2002. The effect of hunger on mating behaviour and sexual selection for male body size in *Gerris buenoi. Anim. Behav.*, **64**: 369–375.

Ortigosa, A. and Rowe, L. 2003. The role of mating history and male size in determining mating behaviours and sexual conflict in a water strider. *Anim. Behav.*, **65**: 851–858.

Phillips, P.C. and Arnold, S.J. 1989. Visualizing multivariate selection. *Evolution*, **43**: 1209–1222.

Pitcher, T.E., Neff, B.D., Rodd, F.H. and Rowe, L. 2003. Multiple mating and sequential mate choice in guppies: females trade up. *Proc. R. Soc. Lond. B*, **270**: 1623–1629.

Poulin, R. 1994. Mate choice decisions by parasitized female upland bullies, *Gobiomorphus breviceps. Proc. R. Soc. Lond. B*, **256**: 183–187.

Schulte-Hostedde, A.I., Zinner, B., Millar, J.S. and Hickling, G.J. 2005. Restitution of mass–size residuals: validating body condition indices. *Ecology*, **86**: 155–163.

Simmons, L.W. 1994. Courtship role reversal in bush crickets: another role for parasites? *Behav. Ecol.*, **5**: 259–266.

Stinchcombe, J.R., Agrawal, A.F., Hohenlohe, P.A., Arnold, S.J. and Blows, M.W. 2008. Estimating nonlinear selection gradients using quadratic regression coefficients: double or nothing? *Evolution*, **62**: 2435–2440.

Uetz, G.W. and Norton, S. 2007. Preference for male traits in female wolf spiders varies with the choice of available males, female age and reproductive state. *Behav. Ecol. Sociobiol.*, **61**: 631–641.

Wagner, W.E., Jr., Smeds, M.R. and Wiegmann, D.D. 2001. Experience affects female responses to male song in the variable field cricket *Gryllus lineaticeps* (Orthoptera, Gryllidae). *Ethology*, **107**: 769–776.

Zar, J.H. 1996. *Biostatistical Analysis*, 3rd edn. Upper Saddle River, NJ: Prentice-Hall.

Zuk, M. 1987a. Variability in attractiveness of male field crickets (Orthoptera: Gryllidae) to females. *Anim. Behav.*, **35**: 1240–1248.

Zuk, M. 1987b. Age determination of adult field crickets: methodology and field applications. *Can. J. Zool.*, **65**: 1564–1566.

Zuk, M. 1988. Parasite load, body size, and age of wild-caught male field crickets (Orthoptera, Gryllidae): effects on sexual selection. *Evolution*, **42**: 969–976.