Male size and sequential mate preference in the cricket *Gryllus bimaculatus*

PHILIP W. BATEMAN, LAUREN N. GILSON & J. W. H. FERGUSON

Department of Zoology and Entomology, University of Pretoria

In crickets, females show preferences for male traits such as body size and either reject outright, take longer to mate with, or remove the spermatophores of nonfavoured males sooner, interrupting sperm transfer. In most mate choice studies, however, empirical tests so far have concentrated on choice between simultaneously presented males, which may not reflect the natural situation. We exposed sequentially to potential mates females that ranged from completely naïve (virgin) to twice mated. Naïve females did not remove the spermatophores of smaller males sooner, but tended (nonsignificant) to reject small males outright. With increasing experience, there was a general decline in spermatophore retention time, but large males were favoured: females either increased retention time when large males succeeded small males or maintained it for the same duration. There were more rejections when small males succeeded large or small males, but fewer when large males succeeded small males. Females appeared to 'bet hedge' at the first copulation, rather than be unable to judge male size/quality; but with increasing experience, their spermatophore retention and rejection behaviour clearly indicated a favouring of large males and an active discrimination against small males. There was a first-male advantage in terms of sperm transfer, but subsequent female behaviour compromised any advantage gained by a small first mate.

© 2001 The Association for the Study of Animal Behaviour

Females of many taxa mate multiply. The existence and advantage of polyandry has been shown in crickets (Tregenza & Wedell 1998), spiders (Watson 1998), prairie dogs (Hooglund 1998), pseudoscorpions (Zeh 1997), lizards (Olsson & Shine 1997), moths (LaMunyon 1997), birds (Birkhead et al. 1993), snakes (Barry et al. 1992; Madsen et al. 1992) and humans (Bellis & Baker 1990).

Most research on mate choice has concentrated on what criteria are used in choosing from a group of potential mates. Females are often the selective sex, preferentially mating with certain males. Generally, however, the empirical evidence has been limited to situations in which a female may choose simultaneously from amongst males and where a direct comparison may be made. This does not necessarily reflect the situation under natural conditions where a female encounters males sequentially. Theoretical papers have suggested a series of rules that females might use to select amongst sequential males.

(1) 'Fixed threshold rule': females mate with the first male that meets the minimum quality criteria (Janetos 1980; Wittenberger 1983).

Correspondence: P. W. Bateman, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa (email: pwbateman@zoology.up.ac.za).

(2) 'Sequential comparison rule': females compare males until the most recent is of lower quality than its predecessor, then mate with the preceding male (Wittenberger 1983).

(3) 'One step decision rule' or 'sequential search rule': females compare males sequentially and mate when male quality is greater than the average male quality expected from continued search (Janetos 1980; Real 1990).

(4) 'Best-of-*n* rule': females sample as many males as possible and mate with the highest-quality ones (Janetos 1980; Real 1990). This rule is the most efficient if there are no costs associated with searching and sampling (Janetos 1980; Real 1990). If there are costs involved, then the 'sequential search' rule is the most efficient (Real 1990).

Empirical studies show that the quality of a previously encountered mate influences female mating decisions with the next potential mate (see Gibson & Langen 1996 for a review). Real (1990, 1991) and Gibson & Langen (1996) suggested that a female's choosiness will be influenced by the cost of searching, the benefits of continued searching (depending on variance in male quality) and a female's own quality (if she is able to judge this). Choudhury & Black (1993) showed that barnacle geese, *Branta leucopsis*, sample several potential mates before

settling on one, using a one-step decision rule, and Dale et al. (1990) showed that female pied flycatchers, *Ficedula hypoleuca*, can return to and select previously visited males, presumably using a best-of-*n* rule. Bakker & Milinski (1991) determined that female sticklebacks, *Gasterosteus aculeatus*, use a 'stochastic decision rule' (similar to the sequential comparison rule), where the probability of choosing a male is directly influenced by the quality of the preceding male. Milinski & Bakker (1992) also showed that choosiness over sequentially presented male sticklebacks declines with increasing sampling costs. Brown (1981) and Downhower & Link (1994) showed that the size of the male mottled sculpin, *Cottus bairdi*, that had previously courted a female appears to influence the probability that she will spawn with the next male that she encounters. Collins (1995) showed that exposure to male zebra finches, *Taeniopygia guttata*, of differing quality influenced mate choice when females were subsequently presented with a pair of males.

In the cricket *Gryllus bimaculatus*, males attract females and solicit copulations by singing. Males also 'posture' (shaking rapidly and orienting towards the female when in close contact), and antennate the female, laying or lashing their antennae over her (contact vibration: Dambach 1989). In crickets, because females mount males during copulation, they ultimately have control over the copulation. In certain species of Orthoptera larger males (Simmons 1986a, b, 1992; Brown et al. 1996), older and more symmetrical males (Simmons 1995; Simmons & Ritchie 1996) and males that win in intrasexual agonistic encounters (Simmons 1986b; Nelson & Nolen 1997) are favoured by females, with song structure and residency in burrows acting as cues for female choice (Simmons 1986b, 1992; Galliart & Shaw 1994; Brown et al. 1996; Gray 1997). Degree of mate preference is considered to be reflected by such criteria as latency to mate (Simmons 1988; Bateman 1998) and complete rejection of some males. Females may further exercise mate preference by adjusting the retention time of the sperm ampulla. Females can interrupt sperm transfer by removing the ampulla and retain those from favoured males for longer (Simmons 1986a; Bateman 1998).

We examined whether, given that female *G. bimaculatus* show mate preference behaviour, this behaviour is influenced by prior experience such that changes in measures of female preference could be seen over the course of several matings. We tested the following predictions about changes in female selectivity over the course of three copulations.

Prediction 1: for first matings, latency to mate will be longer, ampulla retention time will be shorter and number of rejections will be greater for smaller than for larger males. Prediction 2: if the second male is the same size as the first male, latency to mate will be longer and ampulla retention time will be shorter than for the first male. In addition, number of rejections will increase. Prediction 3a: if the second male is smaller than the first, there will be a reduction in ampulla retention time and an increase in latency to mate and number of rejections; 3b: if the second male is larger than the first, it will be

preferred, with either equal or higher ampulla retention time to the first male. Prediction 4a: at the third mating, smaller males will be disadvantaged, either having lower ampulla retention time or higher likelihood of being rejected if preceded by larger males; 4b: larger males will continue to be preferred, but less markedly so, with either equal or higher ampulla retention time than for smaller preceding males, or with equal or nonsignificantly lower ampulla retention than larger preceding males.

We made three assumptions: (1) a longer latency to mate reflects a lower motivation to mate with a male; (2) a longer ampulla retention time reflects a high preference for that male; and (3) that with increasing number of copulations there will be a relative decline in ampulla retention time regardless of male size.

METHODS

We obtained crickets from a colony maintained in the Department of Zoology and Entomology at the University of Pretoria, South Africa. The founders came from various sites in South Africa, mostly from Gauteng Province, but the colony had interbred in the laboratory for several generations. Penultimate and antepenultimate instar female nymphs were isolated from the colonies to ensure virginity, and kept in 2-litre plastic bottles with crumpled tissue paper as a refuge. Penultimate and antepenultimate male nymphs were removed from the colony and, on reaching adulthood, were individually numbered with permanent ink written on a spot of correction fluid on the pronotum, and housed individually in 250-ml plastic jars. To prevent females from using male song to gain experience of the range of potential male quality, we acoustically isolated adult males and females by housing them in separate rooms.

We used nonvirgin males of the same age (10–15 days post final ecdysis, which is when our males began singing consistently) because (1) virgin males may be more incompetent at mating (Simmons 1988) and (2) female crickets prefer older males, regardless of size (Zuk 1988; Simmons 1995).

Unmated males were mated randomly with an adult female from the main colony. These matings are not included in the sequential mating trials. There was a sufficient period between this mating and the first trial mating to allow the male to produce another spermatophore (≥ 24 h). Males and females were kept under a 12:12 h light:dark cycle at 27°C and provided with water-soaked tissue paper and high-protein cereal ad libitum.

Pairs of crickets were placed in plastic containers with a clear Perspex top (16.5 × 11 cm and 4 cm high) lined with tissue paper to facilitate mating. They were allowed to copulate with or reject as mates a series of three males. For her first mating experience, a female was presented with a male either smaller or larger than herself. We defined 'smaller' (S) males as (1) weighing less at the time of mating and (2) having pronotum length and width 1–2 mm smaller than the female with whom they were paired (this size range was chosen to avoid 'mechanical incompetence' in mating caused by a large difference in size). 'Larger' (L) males were defined as (1) weighing more

at mating and (2) having pronotum length and width 1–2 mm larger than the female. We randomly assigned females to one of the eight treatments (LLL, LLS, LSL, LSS, SLL, SSL, SLS, SSS). When a female received two or three 'smaller' or two or three 'larger' males, the males were as closely matched as possible. Each female was used only once. Males were used in no more than three treatments, no more than once in a 24-h period, and never paired with the same female more than once. No male with damaged wings, which might have prevented him from singing normally, was used. No male missing a leg was used, as this appeared to influence mounting success.

For each courtship trial we recorded three measures of female preference for a particular male: (1) duration from first contact between the pair to copulation and spermatophore transfer (latency to mate); (2) duration from spermatophore transfer until the female removed it (ampulla retention time); (3) rejection or acceptance of that male (number of rejections).

Once the female had removed the spermatophore the second or third male was presented to her within 30 min. A male was considered rejected only if he showed courtship behaviour (singing, posturing, antennation), indicating his motivation to mate with a female, yet after 30 min the female showed no interest in mating (no mounts and either aggression towards or escape behaviour from a courting male). We allowed one exception to these criteria: if the rejected male was the female's first mate, that mating was classed as a rejection only if the female subsequently mated with the second mate, presented 20 min later. Males that failed to show any interest in females were not used further. These mistrials were not considered as indicative of females' choice and were discarded from the treatments. Females from these abortive trails were not used in further trials.

We analysed the data with nonparametric techniques. Latency to mate and ampulla retention time of consecutive matings within a treatment (e.g. LSS) were compared with the Wilcoxon signed-ranks test (one tailed; Hollander & Wolfe 1973). A treatment such as LSS therefore required two pairwise comparisons (L with S and S with S) which do not involve independent data sets since both these comparisons involve the same second mating trial (S). We used this method, however, since no alternative statistical approach was feasible.

To compare latency to mate and ampulla retention time of experimental groups within a mating trial (e.g. second matings, comparisons represented by dotted lines in Fig. 1) we used the Mann–Whitney U test (one tailed; Conover 1981). We compared number of rejections between each mating for the different treatments with Fisher's exact test (one tailed). Results are given as means $\pm$ 1 SE. Several of the data sets (e.g. Fig. 1, Table 2 in the Results) are presented as sets of statistical tests. However, these statistical tests test different hypotheses. For instance, the leftmost Fisher's exact test in Table 2 tests the null hypothesis that, during the first mating, large males are preferred above small males. The second most left-hand Fisher value tests the hypothesis that, during the second mating, crickets have the same preference for body size as during their first mating. Therefore
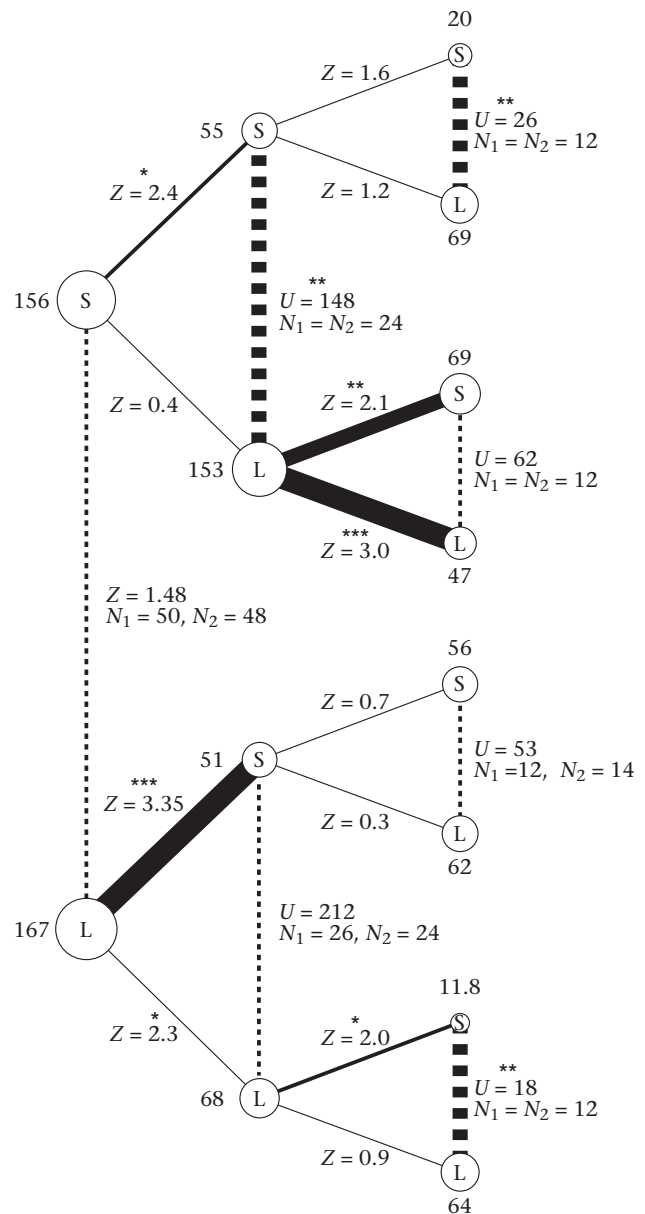

Figure 1. Changes in ampulla retention time with three successive matings for eight treatments. Lines of increasing thickness represent increasing significance. $\cdots$: Tests among treatment groups at first, second, or third mating. U: Mann–Whitney U scores. ——: Tests within treatment groups between successive matings. Z: Wilcoxon signed-ranks Z scores. Circle diameters are proportional to means. Means at each stage are of all Small or Large male ampulla retention times for those positions (e.g. first L is mean ampulla retention time for LLL, LLS, LSL and LSS, first S is mean ampulla retention time for SSS, SSL, SLS and SLL). *$P<0.05$; **$P<0.01$; ***$P<0.001$.

the use of a Bonferroni adjustment on these results is not appropriate.

RESULTS

For all trials combined there was a first-male advantage in terms of ampulla retention time ($\bar{X} \pm SE = 161.7 \pm 24.8$ min) followed by a considerable decline for the

Table 1. Latency to mate (LTM; min), ampulla retention times (ART; min) and number of rejections (NOR; %) for each treatment, over a series of three matings

Mating order		First mating	Second mating	Third mating
LLL	LTM	6.08±1.40 (0–18)	7.41±1.29 (0–14)	8.75±2.86 (1–38)
N=12	ART	133.25±28.70 (0–399)	69.58±15.76 (0–210)	64.25±11.96 (23–164)
	NOR	8.30	16.60	0
LLS	LTM	9.75±2.76 (0–30)	9.58±2.90 (0–30)	1.42±1.05 (0–12)
N=12	ART	111.17±15.82 (0–178)	67.75±20.53 (0–250)	11.83±7.99 (0–74)
	NOR	8.30	25.00	85.00
LSL	LTM	13.08±2.82 (2–30)	5.17±2.32 (0–27)	15.50±1.31 (0–14)
N=14	ART	125.80±16.08 (18–183)	72.3±35.04 (0–389)	62.25±15.00 (0–171)
	NOR	0	57.14	14.30
LSS	LTM	6.17±1.09 (0–13)	2.80±1.14 (0–10)	5.00±2.43 (0–25)
N=12	ART	186.42±30.90 (0–334)	31.42±11.05 (0–96)	56.42±28.07 (0–296)
	NOR	16.60	50.00	66.67
SLL	LTM	5.30±0.89 (0–10)	4.50±1.13 (0–16)	5.42±2.06 (0–27)
N=12	ART	134.92±36.21 (0–367)	176.08±44.42 (0–470)	47.75±9.85 (0–120)
	NOR	16.60	8.30	16.60
SLS	LTM	7.80±2.76 (0–33)	7.75±2.02 (0–25)	6.50±1.71 (0–21)
N=12	ART	83.42±21.11 (0–200)	126.00±38.94 (0–350)	69.80±23.20 (0–255)
	NOR	33.33	8.33	25.00
SSL	LTM	8.08±3.08 (0–30)	4.67±1.69 (0–19)	12.17±2.92 (0–32)
N=12	ART	122.58±48.66 (0–596)	49.50±20.58 (0–195)	69.92±14.61 (0–150)
	NOR	25.00	50.00	8.30
SSS	LTM	8.92±2.34 (0–30)	4.92±1.39 (0–14)	5.50±1.94 (0–20)
N=12	ART	283.50±140.9 (0–1820)	60.50±18.68 (0–158)	20.25±5.65 (0–51)
	NOR	8.30	33.33	41.67
Combined	LTM	8.15±0.82 (0–33)	5.84±0.66 (0–30)	6.28±0.78 (0–38)
N=98	ART	161.70±24.80 (0–1820)	81.65±10.56 (0–470)	50.30±5.90 (0–296)
	NOR	14.55	31.10	32.19

LTM and ART are shown as $\bar{X}$±SE and range (in parentheses). L: large male; S: small male.

second male (81.7 ± 10.5), continuing for the third male (50.3 ± 5.9; see Table 1). Latency to mate was more erratic; females did not necessarily mate with their first mate sooner than with subsequent mates (Table 1), nor did they reject significantly fewer of their first mates compared to all subsequent mates. There was a non-significant trend in number of rejections (mean of first mates=14.5%; subsequent mates=31.6%, $Z= -2.0$, N_1=98, N_2=196, P=0.09). SSS and LLL (i.e. three successive males of the same size) showed a similar pattern in decline in ampulla retention time (first-male advantage), but it was more pronounced in SSS from second to third male (Table 1). Latency to mate showed no significant pattern for either treatment. The pattern of rejections differed between SSS and LLL, with SSS showing a significant increase in percentage of rejections with number of copulations, and LLL showing an increase from first to second male and then zero rejections for the third male (Table 1).

First Matings

Mann–Whitney U tests showed no difference in latency to mate or ampulla retention time between large and small first mates ($Z= -1.1$, N_1=50, N_2=48, P=0.27 and $Z= -1.48$, N_1=50, N_2=48, P=0.138, respectively). The mean percentage of rejections for all large first mates and all small first mates was 8.3 ± 3.4% (range 0–16.6) and

20.8 ± 5.4% (range 8.3–33.3), respectively (Table 1). Although this is not significant (Z=2.5, N_1=50, N_2=48, P=0.11), there is a trend towards more rejections of small first mates (Table 2).

Second Male Same Size as First

For both SS and LL, Wilcoxon tests showed a significant decline in ampulla retention time (Z=2.4, N=24, and Z=2.3, N=24, respectively, both P<0.05). There was no significant change in latency to mate (Z=1.2, N=24, P=0.28 and Z=0.2, N=24, P=0.8, respectively). In all cases (LL and SS) there was a significant increase in the number of rejections (Table 2).

Second Male Smaller than First

For LS sequences, Wilcoxon tests indicated a significant decrease in ampulla retention time (Z=3.35, N=26, P<0.001), a borderline significant decrease in latency to mate (Z=2.0, N=26, P<0.05) and significant increases in number of rejections (Table 2).

Second Male Bigger than First

Where the second male was bigger than the first, no significant difference in ampulla retention time (Z=0.4,

Table 2. Number of rejections as a fraction of the number of relevant trials for each mating treatment

Mating investigated	First mating	LL-, SS-	LS-	SL-	--S	--L
First male						
Large	4/50					
Small	10/48					
Combined data		6/48	2/26	10/24	—	—
Second male						
Combined data	—	15/48	14/26	2/24	14/48	17/50
Third male						
Combined data	—	—	—	—	25/48	6/50
Fisher's exact (one-tailed) P	0.06	0.02	0.001	0.01	0.02	0.01

L: large male; S: small male.

$N=24$, $P=0.72$) or latency to mate ($Z=0.2$, $N=24$, $P<0.8$) was found and there was a decline in number of rejections (Table 2).

Third Matings

Where the third male was the same size as the previous two mates, there was the same pattern for SSS as LLL. There was no continuing significant decline in ampulla retention time from second to third mate ($T=9.0$, $N=12$, $P=0.1$ and $T=27.0$, $N=12$, $P=0.35$, respectively), but for SSS there was a distinct trend, with a drop in ampulla retention time from a mean of 60.5 min (55 for all SS males combined) to 20 min. There was no change in latency to mate (SSS: $T=18$, $N=12$, $P=1.0$; LLL: $T=29.5$, $N=12$, $P=0.76$). In LSS sequences the significant decline in ampulla retention time from first to second mating was not observed, with females maintaining their ampulla retention time from a mean of 31 min (51 for all LS males combined) to 56 min. There was no significant difference in latency to mate ($T=14$, $N=12$, $P=0.58$). There was a continuing trend for an increase in rejections (Table 1). For SLL sequences there was a highly significant decline in ampulla retention time from second to third male ($T=0.0$, $N=12$, $P<0.01$). There was no significant change in latency to mate ($T=24$, $N=12$, $P=0.4$). The trend in increasing number of rejections continued. For both LSL and SSL sequences, Wilcoxon tests showed no significant difference in ampulla retention time: females maintained ampulla retention at the level of the second male (LSL: $T=30$, $N=14$, $P=0.9$; SSL; $T=20$, $N=12$, $P=0.25$). There was no significant change in latency to mate for LSL ($T=29.5$, $N=14$, $P=0.76$), but there was for SSL ($T=9.0$, $N=12$, $P<0.05$). Overall, for --S trials, there was a significant increase in number of rejections and a significant decline for --L (Table 2).

DISCUSSION

Our predictions were supported in that after the first mating, small males were discriminated against in terms of ampulla retention time and number of rejections. Regardless of the size of the first male the female retained the spermatophore for a mean of 156 min. This suggests that at first matings, these naïve females, with no exposure to males or male song, did not use the size of the

male relative to themselves as a criterion for manipulating ampulla retention time. The advantage of being the first male to mate with a female is demonstrated by the drop in ampulla retention time between first and second male, except when a small male was followed by a larger male. In this case, there was an increase in ampulla retention time, suggesting that the female uses the previous male's size as a yardstick to measure the size of the second male.

There was a distinct pattern in the ampulla retention time, but not in the latency to mate. Latency to mate generally did not change significantly, and any statistically significant changes were borderline. In contrast to findings by Simmons (1988) and Bateman (1998; working on *Platygryllus primiformis*), latency to mate does not appear to be a useful indicator of mate choice in *G. bimaculatus*. The following discussion concentrates on the ampulla retention time and the pattern of rejections of males at each stage.

Benton & Evans (1998) pointed out that many studies infer mate choice by correlating a trait such as age, ornament, or body size with a fitness variable such as reproductive success. A significant correlation would suggest the presence of mate choice and no correlation would suggest no mate choice, even though this implicitly requires the female to have 'perfect knowledge' of all potential mates. The female crickets in our study were totally naïve at the first mating, had limited knowledge at the second mating and, therefore, might be expected to show mate choice behaviour (rejections and ampulla retention time) only at the third mating. Indeed, at the first mating, females did not discriminate against smaller males, in terms of ampulla retention time (Table 1) and rejection rate (Tables 1, 2, although there is a trend) either because they did not recognize those males as small or because they were bet hedging. First males therefore had an advantage in ampulla retention time whatever their size. However, the level of rejections at this stage showed a nonsignificant trend towards discriminating against smaller males. The mean percentage of rejections for small males at the first mating was 20% and that for large males was 8%.

When their second male was small, regardless of previous experience, females discriminated against that male in ampulla retention time. When the second male was large, there was a significant decline in ampulla retention

time only if the first male was also large. When a large male succeeded a small male, there was no significant change in ampulla retention time. As the general pattern is a decline in ampulla retention time with successive matings, it is likely that females favour large males after encountering small males, and maintain ampulla retention time despite it being a second mating (Fig. 1, Table 1). The data for rejections support this view: an increase with successive matings, but large males succeeding small males were significantly less likely to be rejected than small males following large males, or even small males following small males (Tables 1, 2).

Although there was not a significant decline in ampulla retention time to a third small male (SSS), there was a considerable trend (from a mean of 55 to 20 min). There was no decline in ampulla retention time when the third male was larger (SSL, in fact a slight increase), suggesting that even at the level of the third mating, females favoured large males based on previous experience. This was also seen in LLL sequences where ampulla retention time was maintained from second to third matings and percentage of rejections fell to zero. There was, however, a highly significant difference in ampulla retention time of small and large males at the third level (Fig. 1, Table 1). Even large males following large males in SLL sequences showed a dramatic drop in ampulla retention time. This could be due more to the females having maintained the second males' spermatophores for almost as long as a first male's, thus compromising the first male's advantage rather than absolute discrimination against the third male.

Simmons (1986a) showed that female *G. bimaculatus* preferred larger males. Bateman (1998) showed that *P. primiformis* individuals of both sexes preferred larger partners. Females of both species removed the spermatophores of smaller males sooner and showed a shorter latency to mate with larger males. However, neither of these studies tested sequential exposure to mates, but rather two or more partners simultaneously. In Simmons' (1986a) study, the results may also have been confounded to a certain extent by male mate-guarding behaviour. Bateman & MacFadyen (1999) found that in the cricket *Gryllodes sigillatus*, females that were mate guarded kept the sperm ampulla for a mean of 10 min longer than unguarded females. None of the female *G. bimaculatus* in our study were mate guarded as we removed the males immediately after sperm transfer precisely to control for this possible influence.

Gray (1997) found that females of the cricket *Acheta domesticus* preferred the song of larger males, and Simmons (1995) showed that *Gryllus campestris* females preferred older males, who were larger and more symmetrical. To a certain extent this choice based on song could be passive (Parker 1983) as the songs of larger males appear louder and are easier to locate. Selection on male body size would therefore be indirect, and postmating cryptic female choice (ampulla retention time) is likely to be more important (Simmons 1992). In our study, unlike that of Gray (1997), the females were acoustically as well as physically isolated from males prior to their matings. Males sang when courting females but the possible influence of the more easily locatable song of the larger males was controlled for and we measured female choice after contact (latency to mate, rejection) and copulation (ampulla retention time). Males were also of the same age. Future work, however, should address the role of prior knowledge of the variety of song types on subsequent mate choice based on physical cues.

Simmons (1986a) suggested that prolonged ampulla retention time and multiple mating with a second male allows the female to bet-hedge: if she mates with a small male first she can dilute his sperm. In *G. bimaculatus* fertilization success by different males seems to be dependent on sperm numbers within the spherical spermatheca. A male that can transfer more sperm fertilizes more eggs. Simmons (1987) also showed that the proportion of offspring sired by a second mating male increased with increasing ampulla retention time, but if the female has mated twice with the first male, there is no second male advantage, unless the second male mates three times with the female. Our study supports this interpretation, with females maintaining or increasing ampulla retention time when large males succeed small males. This is a clear indication of female preference in subsequent matings being based on information required during previous matings. Clearly the four hypotheses we listed in the Introduction are simplistic in the case of *G. bimaculatus* females. It appears that a female uses different rules, depending on the number of matings she has had. As far as size is concerned, it appears that females are not choosy during the first mating (although there is a trend). Subsequent matings, however, appear to fit the fixed threshold rule.

In conclusion, (1) female *G. bimaculatus* discriminate by rejecting smaller males, and show a trend to do so even when totally naïve about males and their variance in size; (2) they bet-hedge by retaining spermatophores of first males for long periods, regardless of male size; but (3) they can attempt to manipulate sperm representation through ampulla retention time in order to favour the sperm of large males. How successful varying ampulla retention time is in favouring or discriminating against the ejaculates of particular males is, however, unknown. The role of latency to mate is still unclear, and does not appear to be useful as an indicator of female preference in *G. bimaculatus*.

References

Bakker, T. C. M. & Milinski, M. 1991. Sequential female choice and the previous male effect in sticklebacks. *Behavioral Ecology and Sociobiology*, **29**, 205–210.

Barry, F. E., Weatherhead, P. J. & Philipp, D. P. 1992. Multiple paternity in a wild population of northern water snakes, *Nerodia sipedon*. *Behavioral Ecology and Sociobiology*, **30**, 193–199.

Bateman, P. W. 1998. Assortative mating by both sexes in the cricket *Platygryllus primiformis* (Orthoptera: Gryllidae; Gryllinae). *Transactions of the American Entomological Society*, **124**, 63–68.

Bateman, P. W. & MacFadyen, D. N. 1999. Mate guarding in the cricket *Gryllodes sigillatus*: influence of multiple potential partners. *Ethology*, **105**, 949–957.

Bellis, M. A. & Baker, R. R. 1990. Do females promote sperm competition? Data for humans. *Animal Behaviour*, **40**, 997–999.

Benton, T. G. & Evans, M. R. 1998. Measuring mate choice using correlation: the effect of female sampling behaviour. *Behavioral Ecology and Sociobiology*, **44**, 91–98.

Birkhead, T. R., Møller, A. P. & Sutherland, W. J. 1993. Why do females make it so difficult for males to fertilise their eggs? *Journal of Theoretical Biology*, **161**, 51–60.

Brown, L. 1981. Patterns of female choice in mottled sculpins (Cottidae, Teleostei). *Animal Behaviour*, **29**, 375–382.

Brown, W. D., Wideman, J., Andrade, M. C. B., Mason, A. C. & Gwynne, D. T. 1996. Female choice from an indicator of male size in the song of the black-horned tree cricket, *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae). *Evolution*, **50**, 2400–2411.

Choudhury, S. & Black, J. M. 1993. Mate-selection behaviour and sampling strategies in geese. *Animal Behaviour*, **46**, 747–757.

Collins, S. A. 1995. The effect of recent experience on female choice in zebra finches. *Animal Behaviour*, **49**, 479–486.

Conover, W. J. 1981. *Practical Nonparametric Statistics*. 2nd edn. New York: J. Wiley.

Dale, S., Amundsen, T., Lifjeld, J. T. & Slagsvold, T. 1990. Mate sampling behaviour of female pied flycatchers: evidence for active mate choice. *Behavioral Ecology and Sociobiology*, **27**, 87–91.

Dambach, M. 1989. Vibrational responses. In: *Cricket Behavior and Neurobiology* (Ed. by F. Huber, T. E. Moore & W. Loher), pp. 178–198. Ithaca: Cornell University Press.

Downhower, J. F. & Lank, D. B. 1994. Effect of previous experience on mate choice by female mottled sculpins. *Animal Behaviour*, **47**, 369–372.

Galliart, P. L. & Shaw, K. C. 1994. The relationship of weight and sound level to continuity of male calling in the katydid, *Amblycorypha parvipennis*. *Journal of Orthoptera Research*, **2**, 43–45.

Gibson, R. M. & Langen, T. A. 1996. How do animals choose their mates? *Trends in Ecology & Evolution*, **11**, 468–470.

Gray, D. A. 1997. Female house crickets, *Acheta domesticus*, prefer the chirps of large males. *Animal Behaviour*, **54**, 1553–1562.

Hollander, M. & Wolfe, D. A. 1973. *Nonparametric Statistical Methods*. New York: J. Wiley.

Hoogland, J. L. 1998. Why do female Gunnison's prairie dogs copulate with more than one male? *Animal Behaviour*, **55**, 351–359.

Janetos, A. C. 1980. Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology*, **7**, 107–112.

LaMunyon, C. W. 1997. Increased fecundity, as a function of multiple mating, in an arctiid moth, *Utetheisa ornatrix*. *Ecological Entomology*, **22**, 69–73.

Madsen, T., Shine, R., Loman, J. & Håkansson, T. 1992. Why do female adders copulate so frequently? *Nature*, **355**, 440–441.

Milinski, M. & Bakker, T. C. M. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proceedings of the Royal Society of London, Series B*, **250**, 229–233.

Nelson, C. M. & Nolen, T. G. 1997. Courtship song, male agonistic encounters, and female mate choice in the house cricket, *Acheta domesticus* (Orthoptera: Gryllidae). *Journal of Insect Behavior*, **10**, 557–570.

Olsson, M. & Shine, R. 1997. Advantages of multiple matings to females: a test of the infertility hypothesis using lizards. *Evolution*, **51**, 1684–1688.

Parker, G. A. 1983. Mate quality and mating decisions. In: *Mate Choice* (Ed. by P. Bateson), pp. 141–166. Cambridge: Cambridge University Press.

Real, L. A. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist*, **136**, 376–404.

Real, L. A. 1991. Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in mate and female fitness. *American Naturalist*, **138**, 901–917.

Simmons, L. W. 1986a. Female choice in the field cricket *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, **34**, 1463–1470.

Simmons, L. W. 1986b. Inter-male competition and mating success in the field cricket *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, **34**, 567–579.

Simmons, L. W. 1987. Sperm competition as a mechanism of female choice in the field cricket, *Gryllus bimaculatus* (De Geer). *Behavioral Ecology and Sociobiology*, **21**, 197–202.

Simmons, L. W. 1988. Male size, mating potential and lifetime reproductive success in the field cricket *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, **36**, 372–379.

Simmons, L. W. 1992. Sexual selection and body size in a natural population of the field cricket, *Gryllus campestris* (L.). *Journal of Orthoptera Research*, **1**, 12–13.

Simmons, L. W. 1995. Correlates of male quality in the field cricket, *Gryllus campestris* L.: age, size, and symmetry determine pairing success in field populations. *Behavioral Ecology*, **6**, 376–381.

Simmons, L. W. & Ritchie, M. G. 1996. Symmetry in the songs of crickets. *Proceedings of the Royal Society of London, Series B*, **263**, 305–311.

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

Watson, P. J. 1998. Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). *Animal Behaviour*, **55**, 387–403.

Wittenberger, J. F. 1983. Tactics of mate choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 435–447. Cambridge: Cambridge University Press.

Zeh, J. A. 1997. Polyandry and enhanced reproductive success in the harlequin-beetle-riding pseudoscorpion. *Behavioral Ecology and Sociobiology*, **40**, 111–118.

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.