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Sequential mate choice in decorated crickets: females use a fixed internal threshold in pre- and postcopulatory choice

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In nature, female crickets often encounter males sequentially, choosing whether to mate with each male they find rather than selecting the most attractive male from a pool of available mates. Upon encountering a male, a female may base her decision to mate on a particular internal threshold or on a relative standard that takes into account the attractiveness of her previous mates. Here, we test whether the attractiveness of a female's previous mating partner influences her behaviour with respect to a second mate in the decorated cricket *Gryllodes sigillatus*. We measured both pre- and postcopulatory female mate choice as well as the effect that postcopulatory mating guarding by males had on females' postcopulatory behaviour. We showed that in both their first and second matings, pre- and postcopulatory mate choice are congruent, as females prefer to mate with, and accept more sperm from, attractive males. However, the outcome of pre- and postcopulatory choice does not depend on the attractiveness of a female's previous mate, suggesting that females employ a single standard upon which their mating decisions are based.

Keywords: crickets; decorated crickets; *Gryllodes sigillatus*; mate guarding; postcopulatory female choice; sequential mate choice; sexual selection

The mechanisms by which females choose their mates have been the focus of a substantial body of empirical work addressing several fundamental issues (Jennions & Petrie 1997). First, a large number studies have attempted to identify the features by which females choose particular males, usually seeking some phenotypic correlate to male mating success (Halliday 1983; Andersson 1994; Jennions & Petrie 1997). Second, with the steady accumulation of evidence suggesting that female choice does not end at copulation (Sakaluk 1997; Edvardsson & Arnqvist 2000; Ward 2000; Simmons 2001), research has also focused on the variety of mechanisms by which females can bias paternity towards certain males after copulation (Eberhard 1996). Finally, a third area of research has focused on the sampling tactics utilized by females to select their mates (Gibson & Langen 1996).

Studies in which females choose simultaneously between two (or more) males often yield important information with respect to the male traits that females prefer, but females in nature often do not assess males in this manner. Instead of evaluating males in a group ('best of *n*' tactic: Janetos 1980 or pooled comparison tactic: Wiegmann et al. 1999), females may encounter males sequentially and thus must make the decision to mate upon contact with each individual male (Janetos 1980; Real 1990; Wiegmann et al. 1999). In this case, females accept or reject males according to an internal standard of acceptability (fixed threshold tactic: Janetos 1980) rather than by comparing males with one another and choosing accordingly.

Even if females do not make a 'best of *n*' decision among potential mates, their mating decisions might still involve considering the characteristics of other males in the population. Females may engage in adaptive searching, adjusting their internal threshold in relation to their previous experience (Jennions & Petrie 1997). For example, females may become more reluctant to mate after mating with an attractive or high-quality male, but less discriminating after mating with a male who is unattractive or of poor quality. Indeed, several studies have shown that females alter their mating decisions based on characteristics of previous mates (sticklebacks: Bakker & Milinski

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1991; sierra dome spiders: Watson 1991; mottled sculpins: Downhower & Lank 1994; zebra finches: Collins 1995; smooth newts: Gabor & Halliday 1997; field crickets: Bateman et al. 2001; guppies: Pitcher et al. 2003).

Mating episodes invariably include both pre- and postcopulatory female choice, but few studies have examined them simultaneously in the context of mate choice tactics (but see Pitcher et al. 2003). This is of particular concern because a female may effectively ameliorate mating decisions she has previously made by accepting more sperm from a current mate than she did from a past mate (Eberhard 1996). Because what is important is how many offspring a particular male sires, postcopulatory biasing of paternity by females must be considered when considering mate choice. Any investigation focussing solely on precopulatory mate choice might: (1) fail to observe a bias towards certain males; or (2) err in the determination of which male a female actually chooses to fertilize her eggs.

The decorated cricket *Gryllodes sigillatus* is particularly well suited to the study of mate choice because its natural history and mating behaviour are well understood, and there are well-defined points in the mating sequence at which both pre- postcopulatory mate choice occur. Furthermore, females in nature often encounter males sequentially, travelling to burrows from which males produce long-range calls. Females travel to these locations in response to these signals, often visiting and mating with one or more males per night (Sakaluk 1987; Sakaluk et al. 2002).

During mating, male *G. sigillatus* transfer a spermatophore consisting of a small sperm-containing ampulla surrounded by a large gelatinous spermatophylax. Female cooperation is required for successful spermatophore transfer, and thus, males cannot impose copulations on females (Brown 1999). After copulation, the female detaches the spermatophylax from the ampulla and consumes it, while the ampulla remains attached and sperm are transferred into the female's reproductive tract. Once the female has consumed or discarded the spermatophylax, she removes the sperm ampulla, terminating sperm transfer (Sakaluk 1984, 1985). As the number of sperm a male transfers is directly related to his share of paternity (Sakaluk 1986; Sakaluk & Eggert 1996), females clearly have the ability to exercise postcopulatory choice by their ampulla-removal behaviour.

The average female in nature mates with several different males during her lifetime (Sakaluk et al. 2002) and laboratory studies have shown that females gain genetic benefits through their polyandrous mating in the form of increased offspring survival to adulthood (Ivy & Sakaluk 2005). Offspring survival in *G. sigillatus* shows significant additive genetic variance, but not nonadditive genetic variance (Ivy 2007), suggesting that females mating with high-quality males can secure 'good genes' for their offspring (Colegrave et al. 2002; Neff & Pitcher 2005).

Here, we investigate both pre- and postcopulatory sequential male mate choice in the decorated cricket *G. sigillatus* to: (1) determine whether a female's mating preference is fixed or depends on the attractiveness of her previous mate; and (2) ascertain whether pre- and postcopulatory preference are reinforcing or antagonistic.

Rather than rely on a priori assumptions about the traits that influence female mating preferences, we used the preferences of females themselves to assess male attractiveness in mating 'tournaments' held prior to the choice trials (Head et al. 2005; Bussière et al. 2006). Male attractiveness was assessed on the basis of females' latency to mating, which has been shown to be a reliable indicator of male mating success in another cricket species (Shackleton et al. 2005). This measure also has the benefit, relative to choice assays, of avoiding the confounding effects of male competitive interactions on female choice. We considered attractive males to be those with whom females quickly mated, and unattractive males to be those with whom females were reluctant to mate. One benefit of attractiveness assays such as these is that they do not attempt to identify any one male trait that females might find attractive, but rather measure attractiveness holistically. Also, because tournaments permit females to determine which males are attractive, they allow for the inclusion of attractive male traits that may not be apparent to human observers.

METHODS

Experimental *G. sigillatus* were the descendants of approximately 500 individuals that were collected in Las Cruces, New Mexico in May 2001. Experiments were carried out between October and December 2004. All crickets were housed in an environmental chamber at 30°C on a 16:8 h light:dark cycle and provisioned with Flukers cricket chow, water supplied in 40-ml plastic tissue culture flasks plugged with cotton dental rolls, and egg cartons to provide shelter and to increase surface area. Moistened peat moss was made available both as an oviposition substrate and as a source of additional water.

Four attractiveness tournaments, each consisting of two rounds of mating, were staged to identify attractive and unattractive males for use in mate choice trials. Males participated in tournaments over a 2-day period, with the final top and bottom 25% of males assigned to experimental females as 'attractive' and 'unattractive', respectively (Fig. 1). In each tournament, 60 males of unknown mating status were randomly selected from the colony 24 h before mating trials and housed together in a large plastic tub (55-litre, 59 × 43 cm and 30.5 cm high). The tournaments proceeded as follows: on day 1, each of the 60 males was placed in a Plexiglas viewing chamber (10.5 × 7.5 cm and 3 cm high) lined with a paper towel and provided with a stock female from the colony. Pairs were observed 1 h into the dark portion of their light cycle under red light to minimize observer interference. We used latency to mating as our measure of attractiveness. Because females rarely mate with males that do not produce courtship song (Adamo & Hoy 1994), we measured latency to mating as the time elapsed from the start of male courtship song until the time at which mating began (i.e. the beginning of spermatophore transfer). Round one (i.e. the first day of mating) concluded when each male had transferred a spermatophore, thus ensuring that the

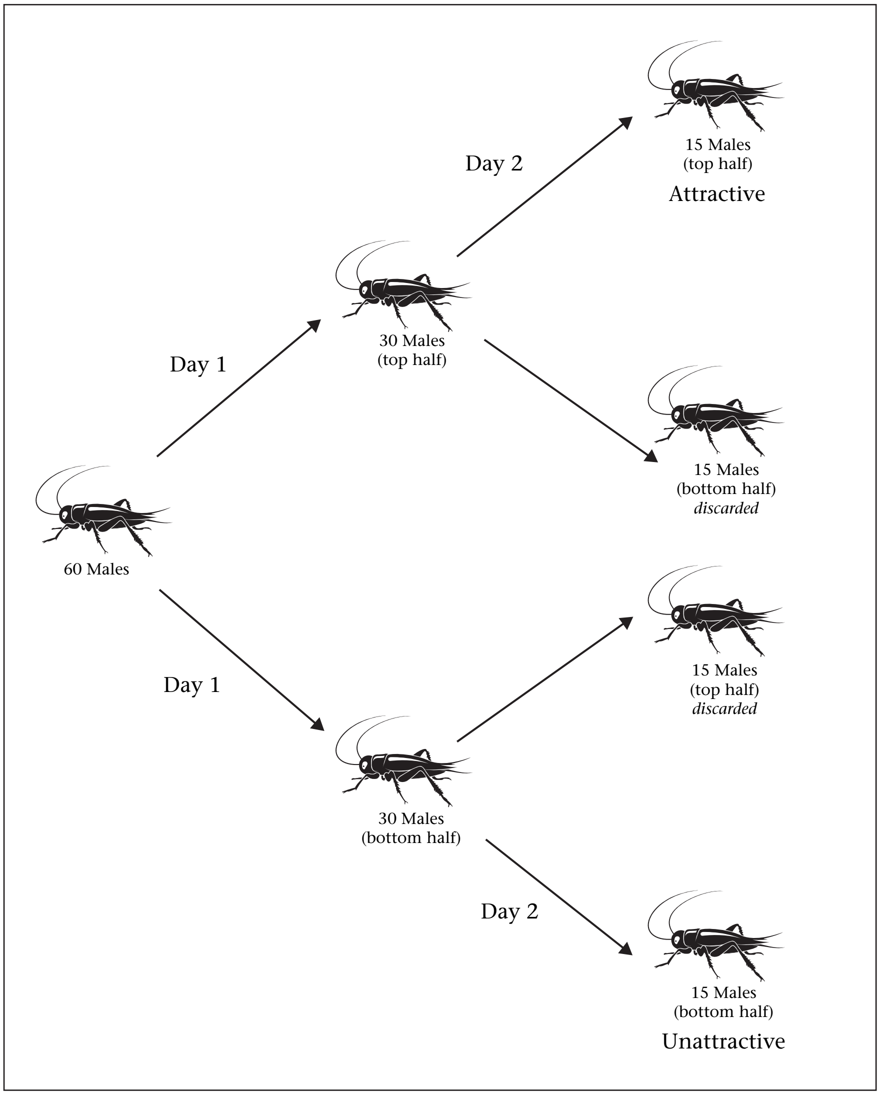

Figure 1. Design of tournaments to determine male attractiveness.

recent mating experience of experimental males was homogeneous.

After this initial round, males were housed individually in 0.47-litre containers. The next day, each male was paired with a different stock female and once again observed until mating occurred. From the 30 males with the shortest latency to mating on the previous day, the 15 with the shortest latencies to mating on the second day were designated as 'attractive'. Likewise, from the 30 males with the longest latencies to mating on the previous day, the 15 with the longest latencies to mating on the second day were designated as 'unattractive'. Males were again housed individually until the commencement of mating trials the following day. Once used in a tournament, males and stock females were not used again.

On the second day of each tournament, 15 experimental females of unknown mating status were randomly chosen from the colony and housed together for 24 h in a large plastic tub. These experimental females were randomly assigned to one of four mating treatments in which they were provided with attractive or unattractive males in different combinations over 2 successive days. In the first treatment, females were given an attractive male with whom to mate on both the first and second days (AA). In the second treatment, females were first provided with an unattractive male and then provided with an attractive male (UA). In the third treatment, females were presented with an attractive male on the first day and presented with an unattractive male on the second day (AU). The fourth treatment presented females with unattractive males on both the first and second days (UU). Fifteen females were included in each treatment. We staged matings in clear plastic shoeboxes (30.5 × 16.5 cm and 8.5 cm high) lined with a paper towel and observed under red light. We used larger arenas in these trials to allow experimental females greater latitude to elude males should they choose to do so (Simmons 1991). For all matings, we recorded the time at which the male began courting, the time at which spermatophore transfer began, the time of successful copulation (i.e. the time at which the spermatophore was successfully transferred) and the time after mating at which the female removed the sperm ampulla.

Latency to mating was calculated as before to serve as our measure of precopulatory choice. We used the duration of ampulla attachment, calculated as the time elapsed from successful copulation (i.e. spermatophore transfer) to removal of the ampulla, as our measure of postcopulatory female choice. Because there is a direct linear relationship between the duration of ampulla attachment and the number of sperm transferred (Sakaluk 1984), the duration of ampulla attachment indicates how many sperm a female accepted from her mate. We censored ampulla attachment duration data at 60 min because attachment durations longer than this are not biologically relevant, as they do not result in increased sperm transfer (Sakaluk 1984).

In an effort to minimize disturbance during the trials, we allowed the male to remain with the female after spermatophore transfer had occurred. Because postcopulatory guarding by male *G. sigillatus* may thwart females' attempts to remove the ampulla (Sakaluk 1991; Frankino & Sakaluk 1994), we also recorded the time at which females first *attempted* to remove the ampulla as an indicator of her 'desired' duration of ampulla attachment. When the 'desired' attachment duration differed from the actual duration (i.e. if the male prevented the female from removing the ampulla), we used the 'desired' duration as our measure of postcopulatory choice because that measure is indicative of female choice without the confounding effect of male coercion.

Statistical Analyses

All data were analysed using the Statistical Analysis System version 9.1 (SAS Institute 2004). We used ANOVA (PROC GLM; SAS Institute 2004) to analyse the effect that tournament and treatment had on latency to mating for both the first and second matings. We employed failure time analysis (Kalbfleisch & Prentice 2002), which permits the inclusion of censored data, to determine the influence of male attractiveness on ampulla attachment duration for both the first and second matings (PROC LIFETEST; SAS Institute 2004). Failure time analysis does not allow for the testing of interactions, so for a female's second mating, we used multiple comparisons to identify differences among the four treatments. For these comparisons, we report medians rather than means, as failure time analysis is a nonparametric statistical method. All statistical tests were two-tailed.

For all analyses, we controlled for multiple tests using permutation adjustments in PROC MULTTEST (Westfall et al. 1999). When comparing groups in their latency to mating, we used *t* tests and resampled the data 10 000 times. For the duration of ampulla attachment, we used a Peto mortality-prevalence test, setting the permutation value at 10 (Westfall et al. 1999).

RESULTS

Our tournaments were successful in producing two groups of males that differed in their attractiveness to females, with attractive males mating more quickly with females than unattractive males (mean ± SE in minutes: attractive: 2.56 ± 0.37; unattractive: 22.09 ± 3.75; two-sample *t* test: Satterthwaite $t_{60.2} = -5.18$, $P < 0.0001$). The tournament from which attractive and unattractive males were derived had no effect on latency to mating (ANOVA: first mating: $F_{3,56} = 0.22$, $P = 0.88$; second mating: $F_{3,56} = 0.88$, $P = 0.46$), nor did tournament influence ampulla attachment duration (restricted likelihood ratio test: first mating, survival analysis test of homogeneity across strata: $\chi^2_3 = 0.86$, $P = 0.84$; second mating, survival analysis survival analysis test of homogeneity across strata: $\chi^2_3 = 0.12$, $P = 0.99$). Hence, female mating preferences were pooled across tournaments for all analyses.

In their first mating, females mated with attractive males sooner than they did with unattractive males (mean ± SE in minutes: attractive: 14.6 ± 1.69; unattractive: 30.93 ± 3.30; two-sample *t* test: Satterthwaite $t_{43.2} = -4.40$, $P < 0.0001$), confirming the results of the attractiveness tournaments. With respect to ampulla attachment durations, 26 of the 60 observations were censored during the first mating (i.e. the ampulla remained attached for at least 60 min, the time required for its complete evacuation). A significantly greater proportion of females mated with attractive males accepted a complete ejaculate compared to those mated with unattractive males (attractive: 63.3% (19/30); unattractive: 23.3% (7/30); likelihood ratio test: $\chi^2_1 = 10.08$, $P = 0.0015$). As might be expected, females retained the ampullae of attractive males longer than those of unattractive males (median ± IQR in minutes: attractive: 60 ± 7.35; unattractive: 29.98 ± 45.28; survival analysis test of homogeneity across strata: restricted likelihood ratio test: $\chi^2_1 = 13.37$, $P = 0.0003$). Only six of 60 females were prevented by their first mate from removing the sperm ampulla when desired, four attractive and two unattractive. For these six females, the average duration of ampulla attachment was nearly 27 min greater than desired, though the variation around this mean was quite large (mean = 26.85, lower 95% CI = −2.886, upper 95% CI = 56.586). Attractive and unattractive males did not statistically differ in their abilities to prevent females from removing ampullae (mean difference ± SE in minutes: attractive: 27.99 ± 15.57; unattractive: 24.58 ± 23.34; two-sample *t* test: $t_4 = 0.12$, $P < 0.91$).

The time to a female's second mating was influenced by the attractiveness of her second mate but not that of her first mate, and there was no interaction between the attractiveness of the first and second mates on a female's latency to mate (Table 1, Fig. 2). Hence, regardless of whether her first mate was attractive or unattractive,

Table 1. Two-way ANOVA of a female's latency to mate as influenced by the attractiveness of her first and second mates

Source	*df*	Mean square	*F*	*P*
First mate	1	68.20	0.23	0.64
Second mate	1	2596.47	8.58	0.005
First mate*second mate	1	711.85	2.35	0.13
Error	56	302.72		

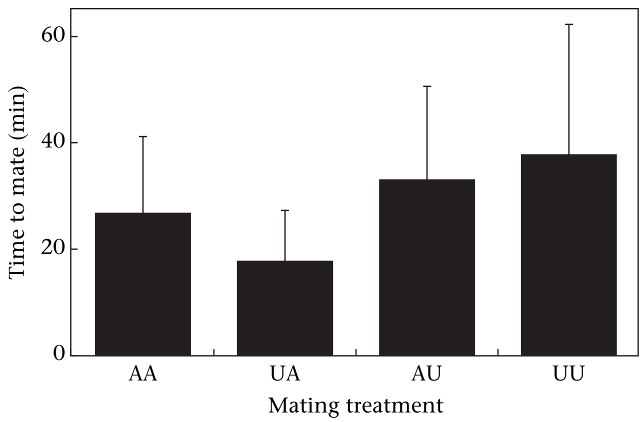

Figure 2. Female latency to mating with the second of two mates in four treatments that varied the attractiveness of females' first and second mates (mean ± SE; A: attractive; U: unattractive). Females mated sooner with attractive males regardless of the attractiveness of their first mates.

a female took longer to mate with an unattractive male than with an attractive male (planned contrast ANOVA: AA and UA versus AU and UU, permutation $P = 0.01$). For ampulla attachment durations in the second mating, 17 observations were censored, five in the AA treatment, 10 in the UA treatment, two in the AU treatment, and none in the UU treatment. Ampulla attachment duration for second matings was significantly influenced by female mating treatment (restricted likelihood ratio test: survival analysis test of homogeneity across strata: $\chi^2_3 = 18.19$, $P = 0.0004$; Fig. 3). Pairwise comparisons showed no evidence of an interaction between the attractiveness of a female's first and second mates on ampulla attachment duration. As with latency to mating, the attractiveness of a female's second mate influenced the duration of ampulla attachment, whereas the attractiveness of a female's first mate did not: females retained the ampullae of attractive males longer than those of unattractive males, irrespective of the attractiveness of their first mates (planned contrast ANOVA: AA and UA versus AU and UU, permutation $P < 0.0001$; AA and AU versus UA and UU, permutation $P = 0.7603$). Second mates prohibited females from removing the ampulla in seven cases. For these seven cases, male guarding resulted in females retaining the ampulla for nearly 24 min longer than desired (mean = 23.91, lower 95% CI = 1.60, upper 95% CI = 46.23). Among females prevented from removing ampullae, those mating with attractive males retained ampullae for longer than those mating with unattractive males, but the variation across individual males was very large (attractive males: mean = 33.21, lower 95% CI = −34.16, upper 95% CI = 100.57; unattractive males: mean = 16.95, lower 95% CI = −19.46, upper 95% CI = 53.35).

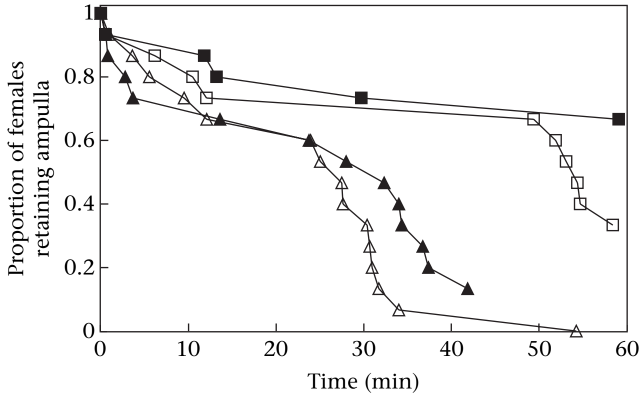

Figure 3. Proportion of females retaining the sperm ampulla in their second mating in four treatments that varied the attractiveness of females' first and second mates (A: attractive; U: unattractive; –□–: AA; –■–: UA; –▲–: AU; –△–: UU). Females retained the spermatophores of attractive males longer than those of unattractive males irrespective of the attractiveness of their first mates.

Overall, female latency to mating was higher in second matings than in first matings (mean difference ± SE in minutes: 6.03 ± 2.77; paired *t* test: $t_{59} = 2.18$, $P = 0.03$). Furthermore, females retained ampullae longer in first matings than they did in second matings, although this difference was not quite statistically significant (6.56 ± 3.83; $t_{59} = 2.18$, $P = 0.09$).

DISCUSSION

Our results add to a growing number of studies demonstrating that females' postcopulatory behaviour reinforces their precopulatory choice of attractive males (Lewis & Austad 1994; Johnson et al. 1999; Pizzari & Birkhead 2000; Evans et al. 2003; Bussière et al. 2006). Female *G. sigillatus* mated sooner and accepted more sperm from attractive males, irrespective of the attractiveness of their previous mating partners, results identical to those reported for another cricket species, *Teleogryllus commodus* (Bussière et al. 2006). These results suggest that upon encountering a male, a female accepts or rejects a male based on an internal threshold of acceptability, not according to the attractiveness of her most recent mate. This does not, however, preclude the possibility that females use other factors to fine-tune their acceptance thresholds, examples of which might include female age (Kodric-Brown & Nicoletto 2001), mating experience (Fleischman & Sakaluk 2004), predation pressure (Forsgren 1992; Godin & Briggs 1996; Gong & Gibson 1996), seasonality (Forsgren 1997), and temperature (Kindle et al. 2006).

The results of our mating trials are consistent with the results of our initial attractiveness assays, suggesting that assessments with respect to male attractiveness are similar across females. However, it is unclear in the case of *G. sigillatus* whether the threshold value that females seem to share is formed by prior experience with members of the population, or whether it is innate. It might prove interesting in future studies to evaluate whether there is a genetic component to female choice in *G. sigillatus*. Female preferences for particular males are often heritable (reviewed in Jennions & Petrie 1997) and may be adaptive, if they result in direct or indirect benefits to females (Iyengar et al. 2002). Alternatively, genetically based female preferences may evolve through Fisherian processes (Lande 1981) or arise as a byproduct of genetically based neurological mechanisms (i.e. sensory exploitation, reviewed in Ryan 1998).

The present study did not attempt to determine which traits females used to determine male attractiveness, and indeed, little is known about precopulatory female preferences in *G. sigillatus* except that female prefer novel males to previous mates (Ivy et al. 2005). In some orthopteran species, females prefer males of larger body size (Gwynne 1982; Simmons 1986; Brown et al. 1996), and females mating with larger males may show higher fecundity (Gwynne et al. 1984; Brown 1997). However, in other orthopteran species, male body size does not seem to greatly affect female choice, and a previous study involving *G. sigillatus* failed to find a precopulatory preference for larger males (T. M. Ivy, unpublished data). Likewise, two other studies involving crickets found no relationship between a male's body size and his mating success (Wedell & Tregenza 1999; Bussière et al. 2006). We think it unlikely that female *G. sigillatus* limit their assessment of males to only one character, but instead use multiple cues to choose their mates (Iwasa & Pomiankowski 1994; Johnstone 1995; Candolin 2003). Thus, although it is not the sole factor determining a male's mating success, it is possible that females evaluate male body size in conjunction with other information when choosing a mate.

While the male traits that influence precopulatory female choice in *G. sigillatus* are not well understood, the targets of postcopulatory choice are better established. There is a strong positive relationship between the time that females spend feeding on the spermatophylax and duration of sperm transfer, and thus, males producing small spermatophylaces transfer fewer sperm than males producing large spermatophylaces (Sakaluk 1984, 1985). As male body size is phenotypically correlated with spermatophylax size, female postcopulatory choice favours large males over small males (Sakaluk & Smith 1988). Male wing morphology also strongly affects the outcome of postcopulatory processes. Males possessing long wings have smaller spermatophylaces and smaller reproductive organs than short-winged males, and therefore transfer fewer sperm than short-winged males (Sakaluk 1997).

Postcopulatory mate guarding functions in many species to protect a male's ejaculate from sperm competition, either by increasing the amount of ejaculate a male transfers or by preventing the female from remating (Alcock 1994). Previous studies evaluating the function of *G. sigillatus* mate guarding behaviour suggest that mate guarding enables males to transfer more sperm (Bateman & MacFadyen 1999) or to exclude potential rivals (Sakaluk 1991; Frankino & Sakaluk 1994; Bateman & MacFadyen 1999). In the current study, mate guarding did not greatly influence females' postcopulatory behaviour with respect to ampulla attachment, as most males were either unable or unwilling to stop females from removing ampullae. However, in the instances where males succeeded in prohibiting spermatophore-removal behaviour, their behaviour did seem to result in the transfer of more ejaculate than if the female had removed the ampulla when she desired, though the low incidence of successful guarding precluded a rigourous assessment. Among the females thwarted in their ampulla-removal attempts, the difference between a female's 'desired' ampulla attachment duration and her actual duration was greater for females mating with attractive males, though the variation among males was quite large (attractive: mean = 30.22, lower 95% CI = 5.11, upper 95% CI = 55.34; unattractive: mean = 19.49, lower 95% CI = −5.07, upper 95% CI = 44.05). Future studies might examine whether male guarding ability is correlated with attractiveness (Bussière et al. 2006).

Females in nature undoubtedly face more complex choices than they do in the laboratory, and it is clear that the costs of mate searching and sampling influence the mating decisions that females make (reviewed in Jennions & Petrie 1997). In the field, *G. sigillatus* females are exposed to increased predation risks through their mate searching behaviour (Sakaluk & Belwood 1984). However, females also gain substantial genetic benefits by mating with multiple males, particularly those of high genetic quality (Ivy & Sakaluk 2005; Ivy 2007). Because females have a great deal to gain by choosing a high-quality mate (more surviving offspring), but a lot to lose by sampling many males (increased chance of predation), we might expect a female *G. sigillatus* to search for a mate only until she finds a male that exceeds her fixed internal threshold of male quality. Indeed, females were more reluctant overall to mate in their second mating than in their first, and this was true for all females except for those that had mated first with an unattractive male and then were presented with an attractive male (see Fig. 2). None the less, females in this study who mated with one attractive male were equally eager to mate with a second attractive male, suggesting, perhaps, that the benefits of obtaining 'good genes' through multiple mating may outweigh the potential costs of mate searching.

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