No Coolidge Effect in Decorated Crickets

Susan N. Gershman & Scott K. Sakaluk

Behavior, Ecology, Evolution and Systematics Section, School of Biological Sciences, Illinois State University, Normal, IL, USA

Correspondence
Susan N. Gershman, School of Biological Sciences, Illinois State University, Normal, IL 61790-4120, USA. E-mail: sgershm@ilstu.edu

Abstract

Female decorated crickets, *Gryllodes sigillatus*, obtain genetic benefits by mating with different males and, when given a choice, prefer novel males over previous mates. It is unknown, however, whether males exhibit a similar preference for novel females. Although female crickets control copulation, there are at least two ways in which males can exercise choice: (1) the amount of courtship directed towards prospective mates and (2) the size of the spermatophore transferred to the female at mating. To determine whether males devote more courtship effort to novel females while controlling for female behavioral cues, male courtship effort toward two dead females, one, a previous mate and the other, a novel female, was measured. To determine whether males manufacture larger spermatophores when paired with novel females, males were mated to novel or previous mates, and the different components of the spermatophore weighed. Males did not spend more time courting dead novel females than previous mates. There was no difference in the latency to remating of males confined with novel females and those paired with previous mates, and there was no difference in the mass of spermatophores transferred to novel and familiar females. Contrary to previous studies in other taxa, this study suggests that male crickets do not prefer novel mates and thus, are not subject to the Coolidge effect. Although mating with novel females may be beneficial to males, selection on males to identify and discriminate against previous mates may be relaxed because of a strong female preference for novel males.

Individuals of both sexes can benefit by mating with multiple partners, females, through the acquisition of genetic benefits that enhance offspring viability (Jennions & Petrie 2000; Mays & Hill 2004), and males, by increasing the total number of offspring sired (Bateman 1948). The ability to identify, and preferentially mate with, novel mates should, therefore, increase an individual's reproductive success. A male preference for novel mates has, in fact, been well documented in a wide array of taxa including mammals (review in Dewsbury 1981), birds (Pizzari et al. 2003), and invertebrates (Arnaud & Haubruge 1999; Koene & Ter Maat 2007; Steiger et al. 2008). The progressive decline in male propensity to mate with a previous partner, combined with a renewed sexual interest in a novel female, is referred to as the Coolidge effect (Dewsbury 1981). However, an important factor overlooked in many of these studies is the possible influence of female behavior. If, in any encounter, the male is novel to the female, so too is the female novel to the male. Experimental results that have been interpreted in support of the Coolidge effect could, therefore, be confounded by female behavior if females are also more sexually receptive to novel males. Conversely, recent studies showing that females of various taxa prefer novel males to previous mates, also have not ruled out a male influence in this effect (Bateman 1998; Archer & Elgar 1999; Eakley & Houde 2004; Ivy et al. 2005; but see Zeh et al. 1998; Newcomer et al. 1999 for notable exceptions).

In the decorated cricket, *Gryllodes sigillatus,* previous work has revealed that, when given a choice, females mate more often with novel males than with previous mates (Ivy et al. 2005), but the extent to which male behavior contributes to this effect remains unknown. Although copulation in crickets is under the control of the female (Loher & Dambach 1989; Zuk & Simmons 1997), there are at least two ways in which males could exercise a choice of females: (1) the amount of courtship they direct towards prospective mates and (2) the size of the ejaculate they transfer to females at mating. With respect to courtship, females will not mount males unless males produce the specific song and quivering side-to-side movements that comprise courtship behavior (Balakrishnan & Pollack 1996); hence, males can influence which females mount them by the relative amount of time they spend courting different females.

In crickets, sperm and accessory gland products are transferred to females in the form of a spermatophore, which remains secured to the female's genital opening outside her body after mating. In other animal species, males can adjust the size of their ejaculate according to their familiarity with a prospective mate even after copulation has begun (Pizzari et al. 2003). However, this is not possible in crickets because spermatophores are manufactured in advance of copulation. So how might male crickets adjust the size of their ejaculate in accordance with their familiarity with a prospective mate? Males begin synthesizing a new spermatophore almost immediately after a previous mating, a process that can take an hour or more (Loher & Rence 1978; Ootsubo & Sakai 1992), and the number of sperm allocated to the spermatophore can be determined fairly early on in the process (Hall et al. 1999). In *G. sigillatus*, the time needed to replace a spent spermatophore is about 3.25 h (Sakaluk 1985), and during that time, a male could easily find himself in close contact with a previous mate depending on his success at mate guarding (Sakaluk 1991), or with a new female if, as often occurs, a different female entered his burrow. Field studies of *G. sigillatus* in outdoor enclosures have shown that: (1) males can be visited by multiple females in the course of the night (Sakaluk 1987), (2) females are more likely to remain in a shelter occupied by a male than a shelter without a male (Sakaluk 1987), and (3) females often mate with more than one male in the course of a night (Sakaluk et al. 2002). The extended close contact with both novel and familiar females, therefore, coincident with the period of spermatophore production, would afford males ample opportunity to evaluate female novelty and adjust their ejaculate composition accordingly.

The spermatophore of male *G. sigillatus* consists of two distinct components, a small, sperm-containing ampulla surrounded by a larger gelatinous mass, the spermatophylax, which is devoid of sperm. The female detaches the spermatophylax from the ampulla with her mouthparts immediately after copulation, feeding on it while sperm are evacuated from the ampulla into her reproductive tract (Sakaluk 1984). After the spermatophylax has been consumed, the female removes and eats the sperm ampulla, terminating sperm transfer. Larger spermatophylaxes take longer to consume and, consequently, males that produce larger spermatophylaxes transfer more sperm and sire more offspring (Sakaluk 1985, 1986). In addition, the amount of sperm contained in the sperm ampulla influences a male's fertilization success because in *G. sigillatus*, fertilizations are determined by the number of sperm a male transfers relative to the numbers transferred by the female's other mates (Sakaluk 1986; Sakaluk & Eggert 1996; Calos & Sakaluk 1998; Eggert et al. 2003). Hence, males paired with novel mates could favor these females through differential investment in their ejaculates in two ways: (1) by producing a larger spermatophylax, resulting in increased sperm transfer (Sakaluk 1985) or (2) by allocating more sperm to the ampulla, leading to a higher fertilization success in the context of sperm competition (Sakaluk & Eggert 1996). Indeed, the possibility of prudent sperm allocation in crickets is well evidenced by studies showing that the number of sperm allocated to spermatophores is influenced by the risk of sperm competition (Gage & Barnard 1996; Schaus & Sakaluk 2001; Thomas & Simmons 2007).

To determine whether males prefer novel females to previous mates, while controlling for the possible influence of differential female responsiveness, we exploited the fact that males will readily court recently killed females. We assessed males' pre-copulatory preferences by simultaneously presenting them with novel females and previous mates and measuring their courtship activity. To determine whether males allocate more resources to spermatophores when paired with a novel female, we confined recently mated males with their previous mates or with novel females, and measured the size of the spermatophylax and the ampulla transferred at their next mating.

Materials and Methods

Decorated crickets, *Gryllodes sigillatus,* were descendents of approx. 500 adult crickets collected in Las Cruces, New Mexico in 2001, and used to initiate a

standing colony of approx. 5000 individuals. The colony has consistently produced at least 150 new adults per week since its initiation, and has not experienced any genetic bottlenecks. Experimental crickets were held in 55-l plastic bins and maintained in an environmental chamber at 28°C on a 14 h light:10 h dark photoperiod. Crickets were provisioned with Flukers® cricket chow (Fluker Farms, Baton Rouge, LA, USA) *ad libitum*, 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 for rearing nymphs. Moistened peat moss contained in small plastic cups was provided as an oviposition substrate and served as a source of additional water.

Experiment 1. Male Courtship Towards Novel Females and Previous Mates

Experimental males and females were removed from the colony and housed separately by sex within 48 h of adult eclosion to maintain their virginity. Seven to 8 days after adult eclosion, males were randomly paired with females in small Plexiglas mating arenas (16 × 30 × 9 cm). Pairs were observed to confirm mating, and were allowed to remain together for 1 h thereafter. Crickets were subsequently returned to individually labeled containers. The following day, females were killed by holding them for 10 min in a −80°C freezer, thawed to room temperature, and posed in life-like postures. Choice trials were staged in which two dead females were positioned 8 cm apart at one end of the long axis of a mating arena, one of which had mated with the focal experimental male the day before, and the other, with a different male (this male was subsequently discarded). The focal male was acclimated to testing conditions for 4 min in a mesh pouch at the end of the arena opposite from the females, and then released into the arena. Preliminary trials revealed that this spatial configuration resulted in males approaching and antennating both females, rather than simply antennating and courting the first female they encountered. Males were observed for 10 min, and the duration of courtship (as evidenced by the production of the courtship song and characteristic body tremulation) directed at each female recorded using EthoLog (http://www.ip.usp.br/ebottoni/EthoLog/ethohome.html), software that converts a personal computer into an event recorder. Male courtship behavior directed toward the dead females appeared to be as vigorous as that shown to live females the previous day, and was qualitatively similar with respect to antenna-

tion, courtship song and tremulation. We staged 31 choice trials, and no male or female was used in more than one trial. To determine whether female mass affected male courtship behavior, females were weighed prior to their first mating.

Experiment 2. The Effect of Partner Novelty on Male Spermatophore Investment

Newly eclosed males were housed with mature females for 6 days to ensure their sexual competency prior to the experiment. To increase male motivation to mate during experimental trials, males were isolated in individual boxes 48 h prior to mating trials. Experimental females were virgin and housed as a group prior to the experiment.

We employed a repeated measures design in which males were randomly assigned to mate either twice with the same female (n = 52), or twice with different females (n = 52). It was necessary to use live females for this experiment because males will not transfer a spermatophore unless they are mounted by a female. Matings were staged in the same Plexiglas chambers used in the previous experiment. Food and water were provided *ad libitum* during experimental trials. Immediately after a male's first mating, the female was removed from the arena, the spermatophore removed from her genital opening, and the two components of the spermatophore (spermatophylax and ampulla) separated and weighed to the nearest .001 μg using a Cahn® microbalance (Cahn Instruments Inc., Beverly, MA, USA). The female was then either placed back with the male with which she had mated (previous mate), or placed in an arena with a male that had previously mated with a different female (novel female). The male and female were allowed to feed and freely interact with one another while the male generated his second spermatophore. Pairs were observed until males mated a second time. As before, the spermatophore was removed from the female immediately after mating, separated into its two component parts, and weighed. The spermatophylax and ampulla from both matings were dried to constant weight at 50°C for 24 h prior to being reweighed.

Results

Experiment 1. Male Courtship Towards Novel Females and Previous Mates

Of the 31 males used in choice trials, 16 males spent more time courting the novel female than the

familiar female, and 12 males spent more time courting the familiar female, a proportion that does not deviate significantly from unity ($\chi^2_{Yates} = 0.32$, $p > 0.5$). Three males did not court either female and were excluded from further analysis. Female mass did not affect which female received more courtship (ANOVA $F_{1,26} = 0.20$ $p = 0.66$).

Males spent on the average a total of 366 ± 33 s ($\bar{x} \pm SE$) courting the dead females in the 10-min trials, 166 ± 30 s courting previous mates (range = 0–569 s) and 200 ± 28 s courting novel females (range = 0–507 s). The difference in the amount of time males spent courting previous mates and novel females (time spent courting novel mate minus familiar mate) (37 ± 51 s) was not significantly different from zero (paired t-test, $t_{27} = -0.70$, $p = 0.49$).
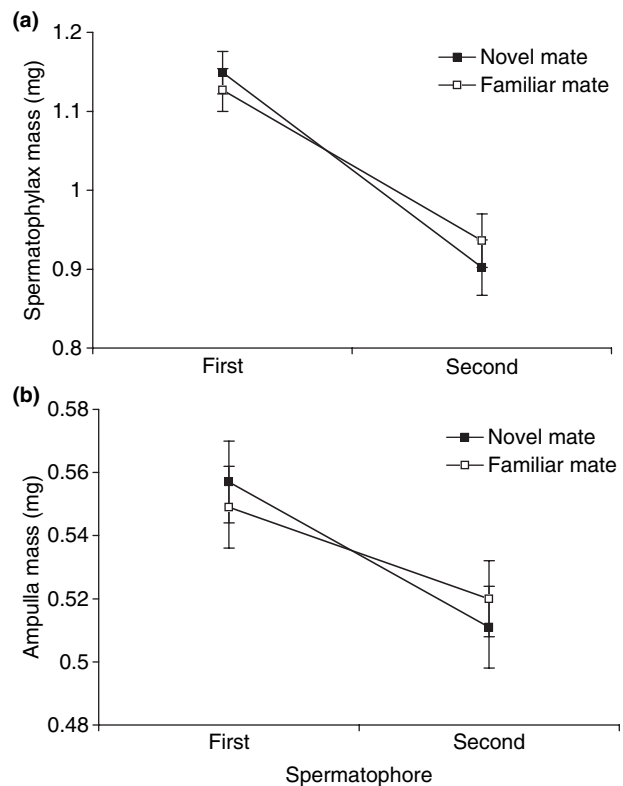
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Thirty-eight of 52 males remated when paired with a previous mate, while 36 of 52 males remated when paired with a novel female. There was no significant difference in the latency to mate of males paired with a previous mate and those paired with a novel female (ANOVA $F_{1,72} = 1.17$, $p = 0.25$). Males paired with previous mates remated 265 ± 11 s ($\bar{x} \pm SE$) after the female was introduced, and males paired with novel females remated 247 ± 10 s after the female was introduced.

There was no significant effect of partner novelty (previous mate or novel female) on spermatophylax dry mass (Fig. 1a; Repeated Measures ANOVA interaction between partner novelty and time $F_{1,76} = 1.6$, $p = 0.21$), or ampulla dry mass (Fig. 1b; Repeated Measures ANOVA interaction between partner novelty and time $F_{1,79} = 0.80$, $p = 0.37$). However, both the spermatophylax and the ampulla of the second spermatophore produced by the male were of significantly smaller mass than those of the first spermatophore (Repeated Measures ANOVA spermatophylax: $F_{1,76} = 97.2$, $p < 0.001$; Repeated Measures ANOVA ampulla: $F_{1,79} = 14.7$, $p < 0.001$).

Discussion

Previous research on *G. sigillatus* has shown that females prefer novel males to previous mates when given a choice (Ivy et al. 2005), a preference that seems adaptive given the well-documented genetic benefits of polyandry in this species (Sakaluk et al. 2002; Ivy & Sakaluk 2005; Ivy 2007). In the present

Fig. 1: The effect of partner novelty on (a) spermatophylax and (b) ampulla mass. Shown are means and standard errors of the mass of first and second spermatophylaxes or ampullae of males paired with novel females (black squares) and those paired with previous mates (open squares).

study, however, male crickets showed no preference for novel females over previous mates, a result that is inconsistent with the Coolidge effect. When presented with a novel female and a previous mate simultaneously, males spent a similar amount of time courting the two females, and when confined with previous mates or novel females, males' ejaculate allocations were similar in both cases. These results are congruent with those found by Newcomer et al. (1999) and Zeh et al. (1998) in which male pseudoscorpions failed to alter spermatophore production or composition in response to partner novelty. We conclude, therefore, that the female preference for novel males documented in our earlier work (Ivy et al. 2005) is not confounded by a male preference for novel females.

Although there was no effect of partner novelty on the size of the spermatophylax or ampulla manufactured by males, spermatophore size varied across successive matings, with second spermatophores of significantly smaller mass than first spermatophores. In light of the experimental design, this difference is

not entirely surprising. Although males had *ad libitum* access to food and water throughout the mating trials, most males chose to remain in close association with females rather than eating or drinking, presumably to engage in post-copulatory mate guarding (Sakaluk 1991; Frankino & Sakaluk 1994; Bateman & MacFadyen 1999). Thus, males likely had fewer resources available with which to produce a second spermatophore.

Female *G. sigillatus* in this study were not faster to mate with novel partners than familiar mates. This result contrasts with the results of a previous study, in which females presented with a previous mate and novel male were more likely to mate with the novel male (Ivy et al. 2005). This apparent contradiction potentially may be explained by a difference in experimental design. In the Ivy et al. (2005) study, females were simultaneously presented with pairs of males, while in this study, a one-choice design was employed. Based on what is known about the reproductive behavior of *G. sigillatus* from field and enclosure studies, it is likely that wild female crickets have the opportunity for both simultaneous and sequential choice (Sakaluk et al. 2002), and females presented with sequential choices may employ a threshold criterion that is less stringent (Ivy & Sakaluk 2007). Indeed, discrimination by females presented with simultaneous choices, absent in sequential preference trials, has also been documented in female guppies (MacLaren & Rowland 2006).

The absence of a Coolidge effect in *G. sigillatus* suggests either that males lack the ability to distinguish between previous mates and novel females, or that they have the ability to do so but do not gain any benefits from discriminating against familiar females in favor of novel ones. It seems unlikely that males cannot distinguish between novel females and previous mates. Ivy et al. (2005) demonstrated that female *G. sigillatus* use self-referent cues to avoid mating with previous mates. During copulation, the female appears to imbue the male with her own 'scent', enabling her to recognize him as a previous mate in later interactions. More recent gas chromatographic analyses of the extracted cuticular hydrocarbons (CHC) of females from each of nine inbred lines have revealed significant genetic variation in the chemical signatures of female *G. sigillatus*, lending support to the idea that females can distinguish between their own chemical cues and those of other females (C. Weddle, unpublished data). While the reliance on unique, self-referent cues by female *G. sigillatus* does not demonstrate that the same is true of males, a recent study of another cricket

species, *Teleogryllus oceanicus*, has reported similar levels of genetic variation in CHC profiles of males (Thomas & Simmons 2008a). In addition, sexual differences in the CHC profiles of males and females have been well established (Tregenza & Wedell 1997; Thomas & Simmons 2008b; C. B. Weddle, C. G. Hamaker, C. Mitchell, J. Hunt, S. K. Sakaluk, unpublished data).

If males can distinguish between previous mates and novel females, why do they not discriminate against previous mates assuming that such a preference would maximize a male's lifetime number of mating partners and, presumably, the number of offspring he sires? For female *G. sigillatus*, there appear to be few benefits to mating more than once with the same male. Ivy & Sakaluk (2005) showed that females mated three or five times to the same males produced fewer offspring than females mated once to each of three or five different males, and subsequent work showed that females accrue significant genetic benefits by mating polyandrously (Ivy 2007). Further, females may incur significant costs of supernumerary matings including risk of predation (Sakaluk & Belwood 1984; Sakaluk 1990), probability of disease transmission (Luong et al. 2000; Luong & Kaya 2005), and wasted time and energy that could be invested in more profitable activities (Daly 1978). Thus, there seems to be ample selective pressure favoring a novel-male mating preference in female *G. sigillatus*. In contrast to females, male *G. sigillatus* do appear to experience a net benefit of remating with the same female compared with foregoing a second mating altogether. Experimental analyses of the paternity of offspring of multiply mated decorated crickets have shown that fertilizations are determined largely by lottery: the number of eggs a male can expect to fertilize is proportional to the number of his sperm stored in the female's sperm-storage organ (spermatheca) relative to those of his rivals (Sakaluk 1986; Sakaluk & Eggert 1996; Calos & Sakaluk 1998; Eggert et al. 2003). This means that any male mating more than once with the same female could expect to increase the number of his sperm represented in her spermatheca, and ultimately, the number of offspring sired with this female. While a male might enhance his fitness by distributing his ejaculates among multiple females, the additional number of offspring sired by mating with a different female might not offset the time and energy expended in seeking out a different female if a recent mate remained nearby.

Finally, it may be that the female preference for novel mates in *G. sigillatus* (Ivy et al. 2005), may

mitigate any selection for a similar preference in males. In crickets, successful copulation requires the female to voluntarily mount the male (Loher & Dambach 1989; Zuk & Simmons 1997), and so too is the amount of sperm transferred under the control of the female via her spermatophore-removal behavior (Sakaluk 1984). Because females are less receptive to previous mates (Ivy et al. 2005), courting males are inevitably more likely to secure matings with novel females than they are with previous mates, so that males can passively obtain the benefits of polygynous matings without any mechanism that functions specifically to promote such matings.

Acknowledgements

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