



Male birch catkin bugs vary copula duration to invest more in matings with novel females



Klaus Reinhold^{a,*}, Leif Engqvist^{a,b}, Albia Consul^a, Steven A. Ramm^a

^a Evolutionary Biology, Bielefeld University, Germany

^b Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Switzerland

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Recent developments in the study of mating behaviour have emphasized the importance of strategic investment of limited reproductive resources. However, in many cases it can be difficult to interpret traits such as copula duration, because they are interacting phenotypes that ultimately depend upon both the male and female mating partner, and the sexes may frequently disagree over the optimal outcome. Here we report the results of experiments designed to establish which sex controls copula duration in the birch catkin bug, *Kleidocerys resedae*, and to test for strategic investment by the controlling sex. First, we found that matings of field-caught individuals were relatively short, but that copula duration increased following a period of sexual isolation, reaching a maximum after 2 days. However, copula duration was again shorter in re-pairings of the same individuals 1 h after their first mating. Because these results could be interpreted as a response to sexual isolation by either sex, we next investigated whether copula duration is under male or female control in this species. Experimental pairings between males and females isolated for 1 h or 48 h in all four possible combinations revealed that copula duration depended strongly on the period of male but not of female sexual isolation, implying that this trait is under male control. Finally, if males mated once were re-paired after 1 h with either the same or a novel (but still recently mated) female, we found that they mated for significantly longer with the latter. Collectively, our results imply that male birch catkin bugs in nature are frequently time-, sperm- or seminal fluid-limited, and that, as predicted by theory, they strategically allocate more of their mating effort and ejaculate reserves to novel females, a form of (cryptic) male mate choice.

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There is increasing recognition that males prudently adjust many aspects of their mating behaviour and ejaculate allocation to maximize fitness returns on their reproductive investment (Dewsbury, 1982; Parker, 1983). Indeed, male mate choice is now recognized as an important aspect of sexual selection in many animal taxa (Bonduriansky, 2001; Edward & Chapman, 2011), potentially leading to sperm limitation for females and sexual conflict over mating decisions (Bro-Jørgensen, 2007; Warner, Shapiro, Marcanato, & Petersen, 1995; Wedell, Gage, & Parker, 2002). However, the optimum mating rate is usually expected to be higher for males than for females, leading to frequent sexual conflict (A. J. Bateman, 1948; Parker, 2006). Even where both mating partners readily agree to mate, the risk of sperm competition means that males then often transfer many more sperm or

other ejaculate components than the female would prefer to receive, creating a further arena for sexual conflict (Edward, Stockley, & Hosken, 2014).

One well-studied phenomenon in the context of male mating selectivity is the Coolidge effect, originally defined in mammals as the restoration of sexual activity among males that had previously reached sexual satiety when presented with a novel female (reviewed in Dewsbury, 1981b; see also e.g. Dewsbury, 1981a; Pierce, O'Brien, & Dewsbury, 1992; Wilson, Kuehn, & Beach, 1963). More generally, males in other vertebrate taxa have also been found to express a preference for novel females (e.g. fish: Kelley, Graves, & Magurran, 1999; Spence, Reichard, & Smith, 2013; birds: Pizzari, Cornwallis, Løvlie, Jakobsson, & Birkhead, 2003; lizards: Tokarz, 2008). Evidence for invertebrates is more limited, but suggests that the novelty of the mating partner may also be an important factor driving male reproductive investment. For example, in the simultaneously hermaphroditic great pond snail, *Lymnaea stagnalis*, the propensity to mate in the male role is increased in situations in which the snail is presented with a novel

* Correspondence: K. Reinhold, Evolutionary Biology, Bielefeld University, Morgenbreede 45, 33615 Bielefeld, Germany.

E-mail address: klaus.reinhold@uni-bielefeld.de (K. Reinhold).

mating partner (Koene & Ter Maat, 2007). Similarly, when presented with a mating opportunity with a novel female, male burying beetles, *Nicrophorus vespilloides*, have shorter mating latencies, a behaviour that has recently been interpreted as a 'Coolidge effect' (Steiger, Franz, Eggert, & Müller, 2008; see also Tan et al., 2013). By contrast, male decorated field crickets, *Gryllobes sigillatus*, show no evidence of differential investment towards novel females, with respect to either courtship effort or spermatophore size (Gershman & Sakaluk, 2009; see also Haederer, Werminghausen, Michiels, Timmermeyer, & Anthes, 2009; Newcomer, Zeh, & Zeh, 1999 for further invertebrate counterexamples). The extent to which male insects respond to female novelty by strategically adjusting aspects of mating effort thus remains an open question, and so far as we are aware no study has investigated potential responses to novel/familiar females with respect to copula duration. In insects, there is often a positive correlation between copula duration and sperm transfer (e.g. Engqvist & Sauer, 2003; Sakaluk & Eggert, 1996; Simmons & Parker, 1992). Furthermore, long copulations are often costly (Scharf, Peter, & Martin, 2013), making copula duration a likely target for strategic male investment (Kelly & Jennions, 2011; Parker & Pizzari, 2010; Wedell et al., 2002).

An inherent problem in studying mating interactions is that the traits that are normally measured, such as mating latency, copula duration or sperm transfer, are interacting phenotypes, i.e. the trait value observed potentially depends upon both the male and the female mating partner, and one cannot simply assume that the outcome reflects the optimal trait value of the focal individual (Edward, Poissant, Wilson, & Chapman, 2014; Hall, Lailvaux, & Brooks, 2013; Krebs, 1991; Moore, Brodie, & Wolf, 1997). In the case of copula duration, there is evidence among insects for high degrees of both male (e.g. dung flies, *Scathophaga stercoraria*: Parker, 1970; Parker & Simmons, 1994) and female (e.g. hangingflies, *Harpobittacus nigriceps*: Thornhill, 1983) control, as well as evidence for mutual control (e.g. fruit flies, *Drosophila melanogaster*: Edward, Poissant, et al., 2014). For any particular species, it is therefore important to understand both which sex is able to control different aspects of mating interactions, and how the controlling sex chooses to invest in mating behaviour or ejaculate transfer across successive mating opportunities that differ in their likely fitness returns. In this study, we investigated these questions, i.e. whether males or females control mating duration and whether males invest more in matings with a novel female, in the birch catkin bug, *Kleidocerys resedae* (Heteroptera; Lygaeidae).

METHODS

Kleidocerys resedae is a widespread, univoltine insect that can often be found in large numbers in early summer, on developing birch catkins, into which the females also lay their eggs. Almost whenever they are observed in the field, a large proportion of individual bugs can be found as mating pairs, indicating that males and females frequently mate and invest a large proportion of the available time in mating behaviour. We collected males and females of *K. resedae* from catkins of birch trees, *Betula pendula*, in the vicinity of the Institute of Evolutionary Biology and Ecology, University of Bonn, Germany during the second half of May. For each of the three experiments described below, bugs were collected fresh from the field and held between mating trials in 60 mm diameter petri dishes at room temperature (approximately 20–21 °C), under ambient light and provided with fresh catkins every second day. To prevent the catkins from drying out, petri dishes were sprayed before use with tap water.

Experiment 1: Sexual Isolation and Copula Duration

To measure the effect of sexual isolation on copula duration, we randomly assigned male and female bugs to one of five treatments, keeping individuals isolated for either 0, 1, 2, 3 or 4 days in their own petri dish. After the appropriate period, we transferred individual males on their own catkin to a petri dish containing a randomly selected female from the same treatment also on her own catkin, and made sure the two catkins were touching each other. In the 'no sexual isolation' treatment (0 days isolated), to control for handling effects we also first collected males and females from the field and separated them into individual petri dishes, putting randomly selected males and females together about 1 h later. Usually about six to 10 petri dishes with paired bugs were observed simultaneously to determine copula duration. To ensure that no start or end of a mating was overlooked, each dish was checked at least every 5 min, and we recorded whether the individuals were mating or not. Individual pairs that were in contact but not yet mating, as well as those that had started mating some time ago, were observed more often. To estimate copula duration, we used the mean of the following two estimates: the temporal interval between the first observation in which the pair were seen mating and the first observation after a mating, and the interval between the last observation before the start of mating and the last observation during mating. The pairs were separated after the mating into their individual dishes and paired again about 1 h later to estimate copula duration for a second mating.

Experiment 2: Control over Copula Duration

Because the results of experiment 1 (see below) could be interpreted as either a male or a female response to sexual isolation, we next investigated which sex controls copula duration in *K. resedae*. To determine whether the period of male or female sexual isolation, or the interaction of the two, influences copula duration, we first isolated a new set of field-collected individuals for 2 days in individual petri dishes. Thereafter, approximately half of the individuals were allowed to mate once to produce a pool of recently mated individuals. About 1 h after these matings, the recently mated individuals (designated '1 h' sexual isolation) and the remaining isolated individuals that had not just mated (designated '48 h' sexual isolation) were randomly assigned to male and female pairs (but avoiding the situation in which the same individuals that had just mated together were paired together again). With this design, approximately half of the individuals belonging to one sex and treatment were paired with members of the opposite sex belonging to the same treatment, and half with members of the opposite sex belonging to the opposite treatment, resulting in a balanced 2 × 2 design with respect to the two treatments (isolated for 48 h versus 1 h) for both sexes. The paired individuals were observed and copula duration was estimated as described for experiment 1.

Experiment 3: Male Response to Female Novelty

To determine whether mating with a novel or the same partner influences copula duration, we first collected and isolated several new individuals for 2 or 3 days in petri dishes with birch catkins. Thereafter we transferred individual males with their catkins to individual female dishes and allowed the bugs to mate. After mating, the individuals were separated again. About 1 h later, two pairs of individuals that had mated at approximately the same time were identified, and both randomly assigned to either a 'same' or 'different' treatment. In the same treatment, males were again put

into the dish of the female with which they had just mated, and in the different treatment the males were instead switched, such that both males were now paired with a novel, yet recently mated, female. The treatments therefore differed in the novelty of the mating partner, but across the experiment all males and females had an otherwise similar mating history at the time of the second pairing. Matings were observed and copula duration estimated as described for experiment 1.

Statistical Analyses

We used ANOVAs to analyse the estimated copula durations in experiments 1 and 2. To achieve normally distributed data, all copula duration data were log-transformed prior to analysis. For experiment 3, we used a *t* test to compare copula durations.

RESULTS

Experiment 1: Sexual Isolation and Copula Duration

Copula duration depended strongly on the period of sexual isolation, with matings between recently field-caught animals lasting approximately 17 min, those between individuals isolated for 1 day lasting approximately 24 min and those between individuals isolated for 2 or more days lasting approximately 40 min (Fig. 1, grey bars), resulting in significant between-day variation in copula duration (ANOVA: $F_{4,91} = 10.59$, $P < 0.0001$). By contrast, when males were given a second mating opportunity 1 h after the first, copula duration was universally shortened to around 15–20 min (Fig. 1, white bars), irrespective of the period of sexual isolation prior to the first mating ($F_{4,71} = 1.17$, $P = 0.33$).

Experiment 2: Control over Copula Duration

Male sexual isolation period had a significant effect on the resulting copula duration (two-way ANOVA: $F_{1,76} = 4.65$, $P = 0.03$), but female isolation period did not ($F_{1,76} = 0.59$, $P = 0.44$), nor was there a significant male*female interaction effect ($F_{1,76} = 1.15$, $P = 0.29$; Fig. 2), indicating male control over this aspect of mating behaviour.

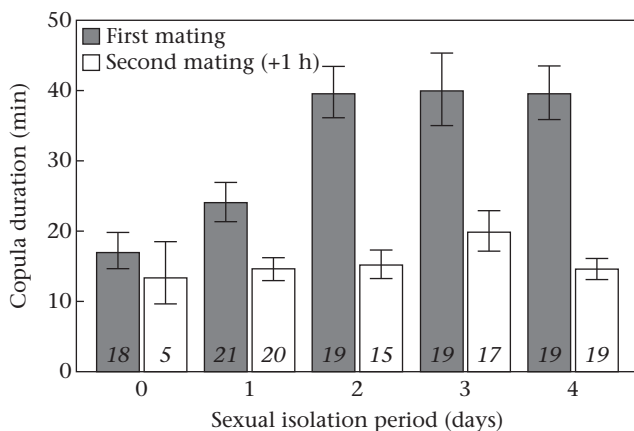


Figure 1. Copula duration in relation to the delay since the last mating: retransformed log (mean \pm SE) copula duration (min) in first matings (grey bars) and subsequent rematings after 1 h (white bars) for pairings of *Kleidocerys resedae* individuals collected from the field and sexually isolated for 0, 1, 2, 3 or 4 days prior to pairing. Sample sizes are given in italics above the x axis. See main text for test statistics on the log-transformed data.

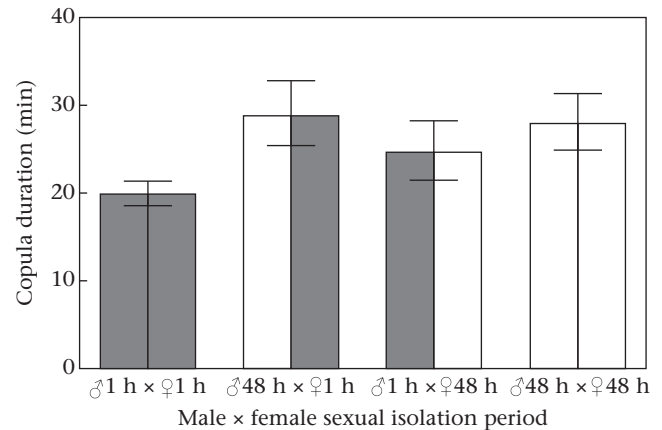


Figure 2. Copula duration in relation to sexual isolation of males and females: retransformed data for log (mean \pm SE) copula duration (min) in matings between male and female *Kleidocerys resedae* isolated for either 1 h or 48 h prior to pairing. $N = 20$ in each treatment group. See main text for test statistics on the log-transformed data. A shaded left half of each bar indicates that the male had been isolated for 1 h prior to the test, and a shaded right half indicates the same for females (i.e. unshaded portions indicate 48 h isolation).

Experiment 3: Male Response to Female Novelty

Males re-paired with a novel partner 1 h after their first mating lasted for, on average, twice as long (mean \pm SE: 30.5 ± 4.6 min) as males re-paired with the same female (15.1 ± 3.1 min; *t* test for samples with unequal variances: $t_{17,29} = 2.52$, $P = 0.02$; Fig. 3).

DISCUSSION

The evolution of strategic male mating investment hinges on three critical assumptions: (1) optimal mating investment causes nontrivial costs to males so that male mating potential is limited; (2) the trait under consideration (e.g. mating latency, copula duration or ejaculate transfer) is under male control; and (3) mating opportunities differ regarding expected fitness payoffs to males. Here we report results consistent with the first of these assumptions and establish the other two attributes with respect to copula duration in birch catkin bugs; we conclude that males invest more in matings with novel females. This is, to our knowledge, the

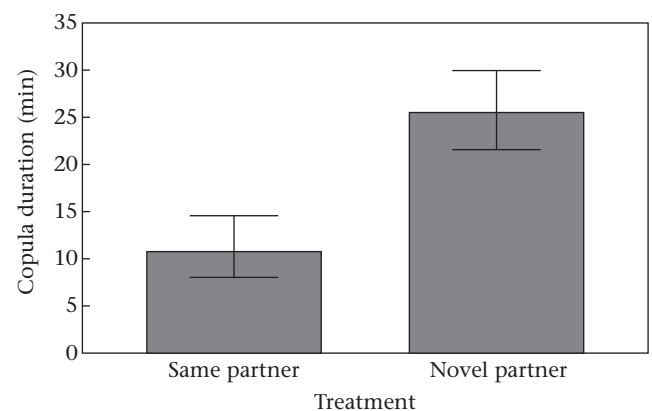


Figure 3. Copula duration in relation to female novelty: retransformed log (mean \pm SE) copula duration (min) in *Kleidocerys resedae* when males were paired with either the same ($N = 12$) or a novel ($N = 16$) mating partner 1 h after a first mating. See main text for test statistics.

first study demonstrating strategic male investment in copula duration regarding female novelty/familiarity in insects, corresponding to earlier reports of similar effects regarding premating preferences (Steiger et al., 2008; Tan et al., 2013). It is thus one of the very few examples in any taxon verifying a 'Coolidge effect' (in the broad sense of a preference for sexually novel females; Tan et al., 2013) after the onset of copula (see also Pizzari et al., 2003).

Copula Duration and Delay since Last Mating

Given the result of experiment 2 that copula duration is largely under male control in *K. resedae*, the most parsimonious explanations for an increasing copula duration with an increasing period of sexual isolation are either that males benefit from investing more time in a single mating when matings are scarce or that ejaculate availability is constrained in this species due to high mating frequencies. The fact that field-collected animals showed very short copula durations, together with the observation that relatively few freshly caught males that had mated once remated after 1 h, also adds to the general impression of males usually being depleted in ejaculate materials. This interpretation relies on the assumption that copula duration accurately reflects ejaculate transfer amount in this species, which it does in many other insects (e.g. Cordes, Yigit, Engqvist, & Schmoll, 2013; Engqvist & Sauer, 2003; Pérez-Staples, Córdova-García, & Aluja, 2014; Schöfl & Taborsky, 2002; Simmons & Parker, 1992), but the dynamics of ejaculate transfer in *K. resedae* are currently unknown. Thus whether the increasing copula duration over the first 2 days of sexual isolation corresponds to the time required for sperm or seminal fluid replenishment (or both) also remains to be determined. Nevertheless, our results suggest a nontrivial cost of matings in birch catkin bugs so that males' potential to invest optimally in matings is constrained. They may thus be selected to invest prudently in matings (see Parker & Pizzari, 2010; Wedell et al., 2002).

Male Control of Copula Duration

Strategic mating investment further requires that males have at least partial control over processes governing insemination. Males usually have a great deal to gain from increased copula duration and sperm transfer, and correspondingly male insects often seem to have a strong degree of influence over copula duration (e.g. soldier flies, *Merosargus cingulatus*: Barbosa, 2011; fruit flies: Krebs, 1991; seed bugs, *Neacoryphus bicrucis*: McLain, 1989; dung flies: Parker, 1970; water striders, *Gerris lacustris*: Vepsäläinen & Savolainen, 1995). Yet, in some of these examples, females also seem to have at least partial control (Edward, Poissant, et al., 2014; Krebs, 1991; Simmons, Parker, & Stockley, 1999), as suggested by Eberhard (1996). Indeed, since extensive mating is often costly to females (Blanckenhorn et al., 2002; Shuker, Ballantyne, & Wedell, 2006), they may benefit if they can retain or regain control, or at least attempt to shorten copula duration. This has been shown for example in bean weevils, *Callosobruchus maculatus*, in this case to reduce injury inflicted by male genital spines (Crudginton & Siva-Jothy, 2000). In other cases females may have almost complete physical control over copulation, and yet males may nevertheless influence its duration. For instance, in many species in which males provide nuptial food gifts, females will terminate copulations as soon as they have consumed the gift (e.g. Thornhill, 1983). Nevertheless, males may influence copula duration by providing larger gifts (Engqvist & Sauer, 2001; LeBas & Hockham, 2005; Sakaluk & Eggert, 1996). Thus, male physical control is not necessarily a requirement for strategic investment, but males must be able to have phenotypic control. In our case, the fact that copula duration closely tracked the male but not female period of sexual isolation in

experiment 2 implies that the male state at the time of mating has a significant influence on copula duration, and in this sense males can be said to control this trait.

Since we showed that male but not female sexual isolation period influences copula duration (Fig. 2), this suggests that males have a dominant effect on copula duration control in birch catkin bugs and increase copula duration adaptively either because they have a larger ejaculate available or because they invest more in a single mating when future matings can be assumed to be less frequent. That males control copula duration is an important result as it would otherwise be difficult to disentangle the effect of male novelty from the effect of female novelty in the subsequent experiment. In fact, this is an acute problem in any experiment testing strategic male mating effort as traits such as mate acceptance, copula duration and sperm transfer are interacting phenotypes potentially depending on the action of both sexes. For instance, an effect of female quality on copula duration and/or sperm transfer may be interpreted as differential male investment, but could equally well result from differential female resistance/receptivity behaviour (see e.g. Engqvist & Sauer, 2003; Pitnick & Brown, 2000 for further discussion). With respect to partner novelty/familiarity, this is of utmost importance: if a female is novel to a male, the male is inevitably also novel to the female (Gershman & Sakaluk, 2009). As polyandry may be beneficial for females (Arnqvist & Nilsson, 2000; Jennions & Petrie, 2000; Simmons, 2005), one would consequently expect them to prefer novel to previous mates (see e.g. Archer & Elgar, 1999; P. W. Bateman, 1998; Eakley & Houde, 2004; Hosken, Martin, Born, & Huber, 2003; Zeh, Newcomer, & Zeh, 1998). Any demonstration of a male Coolidge effect may therefore be confounded by female behaviour if females are more receptive to novel males (and vice versa). Experimental results in support of female preference for novel males or male preference for novel females thus always require additional experiments to allow unambiguous interpretation (e.g. this study; Eakley & Houde, 2004; Ivy, Weddle, & Sakaluk, 2005; Newcomer et al., 1999; Steiger et al., 2008).

Copula Duration with Novel Females

We found that males mated for longer with novel females than with familiar females (Fig. 3). The adaptive significance of this behavioural response to female novelty is currently unclear. Given the relatively short copula duration, in combination with the high frequency of mating pairs found in the field, female multiple mating must be extensive in this species, implying high levels of sperm competition. Thus, it seems reasonable to assume that increasing copula duration may increase the sperm competitiveness of a male's ejaculate. This could, for example, be achieved by an increase in either sperm numbers transferred or seminal fluid transfer, assuming these affect sperm competitiveness in this species. An increased copula duration may also partly function as postinsemination mate guarding, reducing the likelihood of female remating with rival males, as shown for other bug species (Schöfl & Taborsky, 2002; Sillén-Tullberg, 1981).

Furthermore, an increase in copula duration of males paired with novel females requires that males are capable of individual recognition or at least recognition of novel females. We can only speculate as to the proximate cues involved in this process. The most likely candidate signal allowing partner recognition is the cuticular hydrocarbons that have been shown to facilitate discrimination in several different contexts within insects (e.g. partner novelty: Ivy et al., 2005; caste differentiation: Singer, 1998; Steiger et al., 2008; genetic similarity: Thomas & Simmons, 2011). Steiger et al. (2008) demonstrated convincingly that males seem to use the female cuticular hydrocarbon profile to avoid repeated matings with previous mates: males discriminated against

unfamiliar females that had been masked with the same surface profile as familiar females. A cognitively simpler mechanism would be to mark mating partners with one's own cuticular signature or other individual-specific volatile compounds, and such self-referent cues seem to be used by female crickets to avoid matings with familiar males (Ivy et al., 2005).

One aspect of our results remains somewhat puzzling. If males can recognize females with which they have recently mated, and further assuming male control over the termination of matings, why should they then resume mating again soon afterwards with the same female and thereby extend the total copula duration, which they could have done in the first place? One possible explanation for this is that males merely have imperfect knowledge of female identity. Thus, it may be beneficial to mate, and thereby not waste any fertilization opportunities, but to shorten copula duration so as to avoid wasting limited resources. This verbal argument makes intuitive sense, but still needs theoretical consolidation. Alternatively, and especially if there is strong last-male sperm precedence in this species, if females might have mated with other males in the interim, remating with the same female may again be favoured from a male perspective.

Strategic Investment in Copula Duration

Our study adds to growing evidence that male insects strategically adjust their mating behaviour, consistent with the optimal allocation of limited ejaculate reserves (Kelly & Jennions, 2011; Simmons, 2001; Wedell et al., 2002) and the operation of male mate choice (Bonduriansky, 2001; Edward & Chapman, 2011). Strategic adjustment of sperm transfer and/or copula duration has now been demonstrated, for example, in response to sperm competition cues (e.g. Gage, 1991; Schaus & Sakaluk, 2001; Simmons, Craig, Llorens, Schinzig, & Hosken, 1993; Simmons & Kvarnemo, 1997; Wedell & Cook, 1999), female mating status (e.g. Cook & Gage, 1995; Engqvist, 2007; Lorch, Wilkinson, & Reillo, 1993; Lüpold, Manier, Ala-Honkola, Belote, & Pitnick, 2011; Martin & Hosken, 2002; Siva-Jothy & Stutt, 2003; Wedell, 1992, 1998) and female quality (e.g. Engqvist & Sauer, 2001, 2003; Gage, 1998; Krebs, 1991; Lüpold et al., 2011; Parker, Simmons, Stockley, McChristie, & Charnov, 1999; Rönn, Katvala, & Arnqvist, 2008; Xu & Wang, 2009). Yet, to our knowledge, there has been no study demonstrating an effect on male strategic mating effort in relation to female familiarity/novelty in insects. Indeed, there appear to have been surprisingly few studies investigating this issue in any taxon (Kelly & Jennions, 2011; Pizzari, 2002; Wedell et al., 2002). Apart from the study by Pizzari et al. (2003) demonstrating a Coolidge effect on sperm investment in male fowl, *Gallus gallus*, we found only a handful of studies addressing this question, all with 'negative' results (i.e. crickets: Gershman & Sakaluk, 2009; freshwater snails, *Biomphalaria glabrata*: Haederer et al., 2009; pseudoscorpions, *Cordylochernes scorpioides*: Newcomer et al., 1999). This stands in sharp contrast to research on the conventional pre-copulatory Coolidge effect, for which there is in general good evidence for a greater reluctance of males to mate repeatedly with a familiar female (Arnaud & Haubruge, 1999; Dewsbury, 1981b; Koene & Ter Maat, 2007; Steiger et al., 2008). While such overt rejection of familiar females is undoubtedly important, the results of our study emphasize the need to also consider more cryptic aspects of strategic mating effort differentially directed towards novel versus familiar females.

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