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William E. Wagner
University of Nebraska–Lincoln, wwagner1@unl.edu

Andrew R. Smith
University of Nebraska–Lincoln

Alexandra Basolo
University of Nebraska - Lincoln, basolo@unl.edu

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False promises: Females spurn cheating males in a field cricket

William E. Wagner, Jr., Andrew R. Smith, and Alexandra L. Basolo

School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, NE 68588-0118, USA

Corresponding author — W. E. Wagner, wwagner@unlserve.unl.edu

Abstract
Females commonly prefer to mate with males that provide greater material benefits, which they often select using correlated male signals. When females select higher-benefit males based on correlated signals, however, males can potentially deceive females by producing exaggerated signals of benefit quality. The handicap mechanism can prevent lower-quality males from producing exaggerated signals, but cannot prevent cheating by higher-quality males that choose to withhold the benefit, and this poses a major problem for the evolution of female choice based on direct benefits. In a field cricket, *Gryllus lineaticeps*, females receive seminal fluid products from males with preferred songs that increase their fecundity and lifespan. We tested the hypothesis that female behavior penalizes males that provide lower-quality benefits. When females were paired with males that varied in benefit quality but had experimentally imposed average songs, they were less likely to re-mate with males that provided lower-quality benefits in the initial mating. This type of conditional female re-mating may be a widespread mechanism that penalizes males that cheat on direct benefits.

Keywords: sexual selection, cryptic mate choice, direct benefits, deception, field cricket

1. Introduction

Female animals often prefer to mate with males that provide the greatest material benefits (Andersson 1994). For some types of benefits, such as higher-quality care for offspring and beneficial products in seminal fluid, females cannot directly assess benefit quality prior to mating. Instead, they must discriminate between males using signals correlated with benefit quality. This reliance on male signals, however, can favour the production of exaggerated signals (Searcy & Nowicki 2005). The handicap mechanism is thought to be the primary factor that prevents deception by lower-quality males; only males capable of providing higher-quality benefits may be capable of supporting the costs of producing attractive signals (Zahavi 1975; Iwasa *et al*. 1991). But if providing benefits is costly, males that are capable of both producing preferred signals and providing higher-quality benefits might cheat by providing inexpensive, lower-quality benefits (Kokko 1998). The handicap mechanism cannot explain why males that produce attractive signals do not cheat, and this poses a major problem for

understanding why males actually provide direct benefits.

In the variable field cricket, *Gryllus lineaticeps*, males sing to attract females, and females prefer males with higher chirp rates and longer chirp durations (Wagner 1996; Wagner & Basolo 2007). Females directly benefit from mating with preferred males; males with higher chirp rates transfer seminal fluids that increase female fecundity and fertility, while males with longer chirp durations transfer seminal fluids that increase female lifespan (Wagner & Harper 2003). Females will mate one or more times with a male (Wagner *et al*. 2001) before leaving to mate with other males on other nights. We tested the hypothesis that conditional female re-mating penalizes cheating males. This hypothesis has received little attention, but selection may often favour benefit-dependent female behavior. For example, when a male provides a lower-quality benefit in an initial mating, a female may refuse to re-mate because the benefits provided do not compensate for the predation risk associated with being near the male. This type of behavior would tend to penalize males that provide lower-quality benefits because they will transfer fewer sperm and thus experience reduced success in sperm competition. While we cannot use direct manipulations in *G. lineaticeps* to force males to provide different quality benefits, we can impose song phenotypes on males that differ, on average, in benefit quality. To test whether female re-mating behavior penalizes cheating males, we thus paired females with muted males of known singing behavior and broadcast an average song type. All females thus heard the same song but were paired with males that naturally varied in benefit quality. We then measured how benefit quality affected a female's probability of re-mating with a male.

2. Material and methods

The animals used were laboratory-reared descendants of females collected from Academy, California (see Wagner & Harper (2003) for rearing methods). Females were used in trials 7 days following their final moult, and males 6-12 days following their final moult. All crickets were virgins at the start of the experiment.

We used male chirp rate as an index of the reproductive benefit a male would provide, and chirp duration as an index of the lifespan benefit (see Wagner & Harper (2003) for details on song recordings and analyses). Following a song measurement, we weighed and muted the male by sealing its forewings with beeswax. At the start of a trial the following day, we weighed a randomly selected female and acclimated it in a mating arena for 15 min. We then introduced the muted male and began broadcasting an average replacement song. We recorded the time at which the male started courting (defined by body movements), and the time of mating (successful transfer of a spermatophore). When a mating occurred, we placed a screen enclosure around the male and halted the song broadcast. Since we were interested in female responses to male seminal fluid benefits, we removed the spermatophore 30 min after mating (when females begin to remove spermatophores themselves) to prevent spermatophore consumption. Then 90 min after mating, we released the male and resumed the song broadcast. If the pair re-mated, the time of re-mating was recorded. If the pair did not re-mate within 90 min, the trial was halted and the female was recorded as not re-mating. Three trials were excluded from analysis because males did not attempt to court.

The replacement song consisted of a loop of 4 s of calling song followed by 4 s of courtship ticks (Wagner & Reiser 2000). For the calling song component, a natural chirp was digitized at 44 kHz and a 15 ms pulse was used to build synthetic chirps (chirp duration = 148 ms, chirp rate = 3 chirps s^{-1}). For the courtship song component, a natural high-intensity tick was digitized at 44 kHz and a tick that was 9 ms in duration was used to build synthetic courtship song (tick rate = 5 ticks s^{-1}). The courtship ticks were 40% of the amplitude of the calling song chirps.
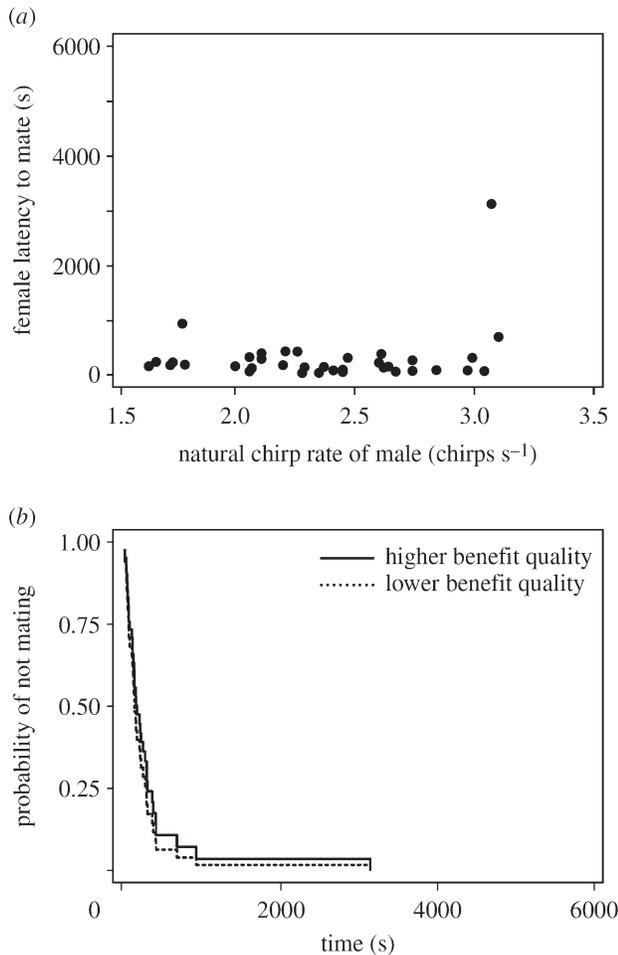
(*a*)

(*b*)

Figure 1. Initial responses of females to males that varied in benefit quality. (*a*) Relationship between natural male chirp rate (which is positively correlated with the quality of the reproductive benefit) and female latency to initially mate. (*b*) Estimated mating functions (lognormal hazard functions) for females that encounter a male that provides a higher-quality reproductive benefit (chirp rate = 3.0 chirps s^{-1}) and a lower-quality reproductive benefit (chirp rate = 2.0 chirps s^{-1}). These functions are based on the observed relationship between chirp rate and female latency to mate, and the two chirp rates were chosen for illustration because they are near the upper and lower extremes for males in our sample.

Females might re-mate faster with higher-benefit males because, as non-virgins, they assess uncontrolled (non-song) traits correlated with benefit quality they did not assess as virgins. We thus conducted a control experiment in which a female's response to a male of known song phenotype was tested after an initial mating to a different male. This experiment was identical to the primary experiment, except that we released a new muted male 90 min after the initial mating instead of the original male.

Data were analyzed using Cox regression, which allows the inclusion of data from females that did not re-mate within 90 min.

3. Results

Females did not initially mate faster with muted males that normally produce higher chirp rates and provide higher-quality reproductive benefits (*n* = 36, *z* = -0.55, *p* = 0.582; figure 1), or that normally produce longer chirp durations and provide higher-quality lifespan benefits (*n* = 36, *z* = -0.95, *p* = 0.342). Thus, prior to receiving male benefits, virgin females did not appear to discriminate among males based on uncontrolled traits correlated with chirp rate or duration.
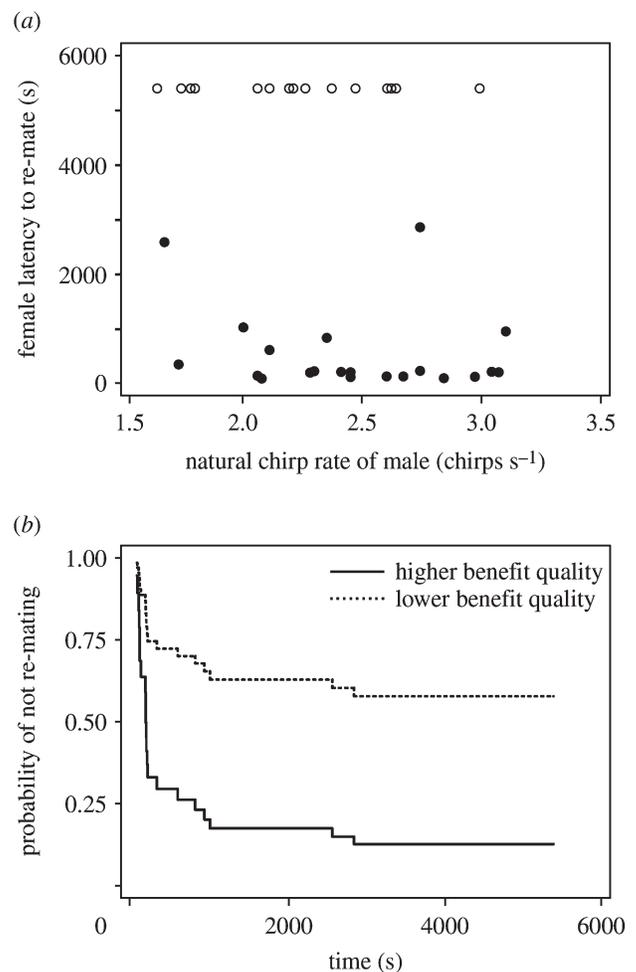
(*a*)

(*b*)

Figure 2. Responses of females, following an initial mating, to males that varied in benefit quality. (*a*) Relationship between natural male chirp rate (which is positively correlated with the quality of the reproductive benefit) and female latency to re-mate. Filled circles, females that re-mated within 90min; open circles, females that failed to re-mate within 90min. (*b*) Estimated re-mating functions (lognormal hazard functions) for that mate with a male that provided a higher-quality reproductive benefit (chirp rate = 3.0 chirps s^{-1}) and a lower-quality reproductive benefit (chirp rate = 2.0 chirps s^{-1}).

Following the initial mating, females were significantly more likely to re-mate with muted males that normally produce higher chirp rates and provide higher-quality reproductive benefits (*n* = 36, *z* = 2.21, *p* = 0.027; figure 2). Females were not, however, more likely to re-mate with muted males that normally produce longer chirp durations and provide higher-quality lifespan benefits (*n* = 36, *z* = 1.45, *p* = 0.146).

These results are consistent with the hypothesis that females assessed benefit quality following the initial mating. It is possible, however, that females responded to other male traits. First, they might have assessed how quickly a male transferred a spermatophore in the first mating trial once it started courting (i.e. some aspect of male performance). There was no effect, however, of initial transfer latency on the time of re-mating (*n* = 36, *z* = 0.71, *p* = 0.481). Second, they might have assessed male size in the initial mating trial. There was no effect, however, of male mass (*n* = 36, *z* = 0.38, *p* = 0.481) or the difference in the male

and female mass ($n = 36$, $z = -0.85$, $p = 0.395$) on the time of re-mating. Third, although virgin females did not appear to assess uncontrolled male traits, they might have done so after the first mating when they were no longer virgins. Following an initial mating, however, non-virgin females did not mate faster with new muted males that normally produce higher chirp rates and provide higher-quality reproductive benefits ($n = 25$, $z = 0.27$, $p = 0.784$).

4. Discussion

Much of the recent work on the evolution of female preferences has focused on indirect genetic benefits. Higher-quality males cannot cheat on genetic benefits, providing lower-quality genes to offspring. Higher-quality males can, however, cheat on direct benefits when females use proxies to assess benefit quality. One hypothesis for why higher-quality males provide benefits, instead of cheating, is that they profit from doing so. For example, male benefits may increase the number of eggs available for fertilization (Gwynne 1988a; Andrade 1996) or offspring fitness (Gwynne 1988b). When females mate with multiple males, however, a male's investment can go to the production of offspring they do not sire, reducing the benefits of investing in females or offspring (Markow 1988; LaMunyon & Eisner 1993).

Our results are consistent with an alternative hypothesis: female behavior penalizes males that cheat. Female *G. lineaticeps* appear to assess benefit quality after an initial mating, and then selectively re-mate with higher-benefit males. This type of cryptic choice (Thornhill 1983; Eberhard 1996) should penalize males that provide lower-quality benefits because they should transfer fewer sperm and have reduced success in sperm competition. How females assess benefit quality is not known, but gene regulation in female insects is known to change in response to seminal fluid proteins (McGraw *et al*. 2004). These results do not preclude the possibility that males also profit from providing direct benefits to females outside the context of female re-mating, and that male benefits and female behavior jointly disfavor cheating.

Conditional female mating behavior based on benefit quality may be a general mechanism that favours the evolution of direct benefits. It has been suggested, for example, that males showing greater parental care may have enhanced paternity in future broods (Kvarnemo 2006). Caring males may have higher paternity in future broods because females are more likely to re-pair with them. While female behavior may impose costs on cheating males, this does not necessarily mean that males will never benefit from cheating. For example, the cost of siring fewer of a female's offspring might be outweighed by the benefit of investing more in attracting additional females (Kokko 1998). Nonetheless, female behavior may be an important factor affecting whether males provide direct benefits.

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