

Mate choice by female crickets is influenced by predation risk

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(Received 20 March 1992; initial acceptance 8 May 1992;
final acceptance 11 July 1992; MS. number: AS-876)

Recent models for the evolution of female choice critically depend on the specific 'decision rules' females use to discriminate among potential mates, yet these rules are poorly understood (Lande 1981; Heisler et al. 1987; Kirkpatrick 1987a; Moore & Moore 1988). Specifically, we do not know whether females adjust their mating decisions in response to the predation risk involved in travelling towards prospective mates (Heisler et al. 1987; Kirkpatrick 1987b; Partridge & Endler 1987). However, animals adjust other types of behavioural decisions in response to predation risk (Lima & Dill 1990), and theory predicts comparable adjustments in mating decisions (Wilson & Hedrick 1982; Real 1990). Here, we present experimental evidence that female crickets, *Gryllus integer*, make trade-offs in their mating decisions between preferences for certain male traits, and the predation risk associated with travelling towards males with those traits.

Male *G. integer* attract sexually receptive females by calling with a rapid trill. In a Californian population, males differ from one another in their durations of uninterrupted trilling (calling-bout lengths; Hedrick 1986). Previous studies (Hedrick 1986, 1988) show that differences among males in calling-bout length are heritable, and females use calling-bout length to discriminate among potential mates, preferentially moving towards calls with longer bouts.

We used phonotaxis experiments to examine whether female *G. integer* would make trade-offs between their preference for long-bout calls and their risk of predation in travelling towards those calls. Mate-searching exposes female crickets to predation risk (Sakaluk & Belwood 1984), and risk is generally higher in open areas than in covered areas because crickets are often eaten by visually-hunting predators (e.g. geckos: Sakaluk & Belwood

1984; toads: personal observation). Correspondingly, female crickets are reluctant to cross open areas, and prefer to travel through cover or crevices. We conducted phonotaxis experiments inside a large, screened experimental arena (160 × 60 × 60 cm high) and used differences in cover within this arena to alter the apparent risk of predation involved in travelling towards different male calls (Fig. 1). Male calls were broadcast at matched, natural sound intensities (72 dB at 1 m) from two Tandberg speakers located at opposite ends of the arena. Cover (7 cm high) was provided on one end, and extended partially (16%, 33%, 50%) or entirely (100%) to the central zone of the arena from one endscreen. Cover consisted of folded black fibreglass netting, containing multiple crevices through which females could travel. We placed a virgin female inside a small chamber (6 × 6 × 6 cm) made of wire screening, with holes at either end. This was placed under a screen holding device at the arena centre, blocking the female's exit. After 3 min we began simultaneous playbacks of alternative male calls from the speakers. After 5 min of playback we raised the holding device, allowing the female free access to the arena for 15 min, during which playbacks were continued. We scored a positive response only if the female left the chamber, walked down the arena, and contacted one endscreen.

Each virgin female ($N = 78$) was tested only once (3–4 weeks post-maturation) except where noted, and was unrelated to other females and recorded males. All crickets were offspring of field-caught Californian mothers, and had heard conspecific calls prior to testing. The arena end with cover and that from which particular calls were played were randomized throughout experiments. Cover was washed and the arena bottom lined with clean paper between trials to eliminate odour cues. Light level during trials was 12–14 lx (arena centre); temperature was 28°C.

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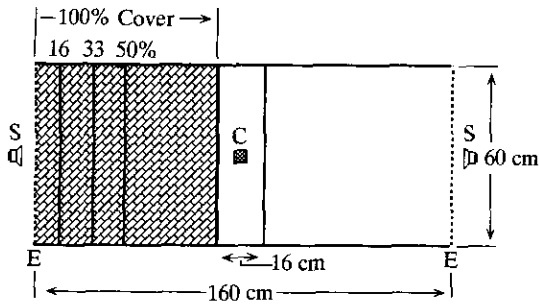


Figure 1. Diagram of experimental arena. Cover extended partially or entirely (100%) to the central zone from one endscreen (E). A female was placed inside a small chamber (C), under a screen holding device (arena centre). Playbacks were conducted from two speakers (S) located at opposite ends of the arena.

As judged by female responses in control experiments, the netting did not appreciably attenuate or degrade sound signals. We made two different recordings at the arena centre of single calls broadcast from one speaker. One recording was made with no cover present; the other with the call broadcast through 100% cover. When offered a choice between these two recordings of a call (no cover present), 14 females did not discriminate between them: seven chose one recording; seven chose the other.

Initially, no cover was placed within the arena, and females were offered a choice between a long-bout and a short-bout call. All 12 females tested moved towards the long-bout call (binomial test, $P < 0.001$), confirming earlier work (Hedrick 1986).

Next, females were offered a choice between either two identical short-bout or two identical long-bout calls, one call played across open space and the other through 100% cover (extending to the arena centre from one endscreen; Fig. 1). Calls were played simultaneously but slightly out of phase with one another, so that periods of calling and non-calling did not precisely coincide. All females ($N = 11$) tested with identical short-bout calls moved to the endscreen in cover ($P < 0.001$), as did seven of seven females tested with identical long-bout calls ($P = 0.008$). Thus, when calls did not differ, females preferred to move through cover versus open space to locate mates.

To examine whether females would trade off their preference for longer bouts against their preference for cover, we gave 12 females a choice between moving across open space towards a long-bout call, or through 100% cover towards a short-

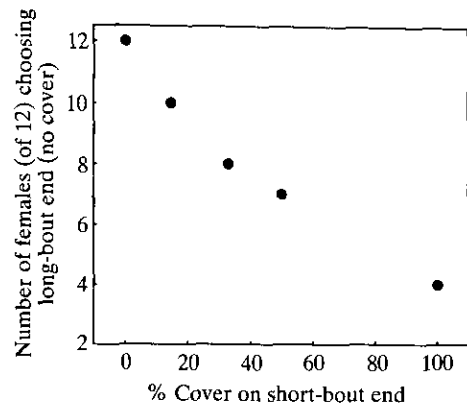


Figure 2. Female choices in phonotaxis experiments. In each of five experiments, 12 different females were tested (total $N = 60$). For each experiment, the number of females choosing the long-bout (preferred) call in the open is plotted against the per cent cover provided on the short-bout end of the arena. The number of females out of 12 choosing the long-bout call progressively decreased as the per cent cover on the short-bout end increased ($r = -0.98$, $P < 0.01$).

bout call. If cover affects mating decisions, we expected some females to 'compromise' and choose the short-bout call in cover. This expectation was met: only four of 12 females moved across open space towards the long-bout call, whereas the other eight moved through cover towards the short-bout call (Fig. 2).

To confirm that females who had chosen the short-bout call ($N = 8$) had made trade-offs between preferences, we re-tested six females, offering them a choice between a short-bout and long-bout call with no cover in the arena. (Two females died before re-testing.) If females had made trade-offs, we expected them now to choose the long-bout call. All six females did so ($P = 0.016$).

Finally, we examined whether cover would affect mating decisions when differences in cover between ends of the enclosure were less extreme. Females were offered a choice between a short-bout and a long-bout call in three experiments, differing only in the amount of cover provided on the short-bout end. Cover extended either 16, 33, or 50% of the way to the arena centre from the endscreen (Fig. 1). In each experiment, 12 different females were tested. Our results (Fig. 2) revealed a clear relationship between the amount of cover provided on the short-bout end of the enclosure, and the number of females moving in that direction. As progressively

more cover was placed on the short-bout end, more females approached that end, and fewer approached the long-bout call (Fig. 2). Thus, our experiments demonstrate that female crickets adjust their mating decisions in response to differences in cover (and the apparent risk of predation) along paths to prospective mates.

Most studies of the relationship between mating behaviour and predation risk have examined how mating activity affects predation risk, yielding mixed results: mating activity may either increase (Lima & Dill 1990) or decrease (Gwynne 1989) vulnerability to predators. In contrast, few studies have examined whether predation risk itself affects mating activity (Sih *et al.* 1990) or mate choice. None the less, many authors (Wilson & Hedrick 1982; Partridge & Endler 1987; Lima & Dill 1990; Real 1990; Sih *et al.* 1990; Magnhagen 1991) have predicted that predation risk should influence mate choice. Our experimental study demonstrates that differential predation risk can substantially alter female mating decisions.

Moreover, our results indicate that females may not mate with the preferred male phenotype (or genotype) when considerations such as predation risk enter into mating decisions. These findings support predictions from models of mate-searching (Wilson & Hedrick 1982; Parker 1983; Real 1990) that search costs (e.g. time, energy, predation risk) will influence mate selectivity, and emphasize that search costs warrant future attention. To date, few empirical studies have carefully considered connections between search costs and mate selectivity (Real 1990), or attempted to quantify these costs (Heisler *et al.* 1987; Price *et al.* 1987; Wilkinson *et al.* 1987; Real 1990). Similarly, models for the evolution of mate choice rarely incorporate search costs (Andersson 1986; Kirkpatrick 1987b; Pomiankowski 1988; Magnhagen 1991). Adding costs to models, however, can have dramatic effects on female selectivity and evolutionary outcomes (Lande 1981; Kirkpatrick 1987b; Pomiankowski 1987; Real 1990; Maynard Smith 1991). Clearly, if costs of choice can influence the reproductive success of different male genotypes in populations, they can influence the evolution of those populations. Our ongoing field research suggests that because of spatial heterogeneity in cover among male calling sites, such costs may operate in Californian *G. integer* to permit the persistence of short-bout genotypes, and therefore the persistence of genetic variation. Thus, further research in this

and other populations on how predation risk and related search costs affect mate choice should prove rewarding.

We thank A. Fraser for the figures, E. Temeles for discussion and advice and C. Boake, A. Moore, R. Rutowski, B. Sullivan, J. Stamps and M. Zuk for comments. This research was supported by NATO/NSF and NSERC (Canada) fellowships to A.V.H. and an NSERC (Canada) grant to L.M.D.

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