

**Sex can be dangerous:  
Acoustically-orienting parasitoids on field  
crickets (Orthoptera: Gryllidae)**

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The Orthopterists' Society generously awarded me grants in 1995 and 1997 to conduct research on *Teleogryllus oceanicus* (Orthoptera: Gryllidae) on the Big Island of Hawaii. Here I report results to date from fieldwork conducted in the past few years.

*Teleogryllus oceanicus* is native to the Pacific Islands and Australia and has been introduced into Hawaii (Kevan 1990; Otte and Alexander 1983). Like other field crickets, males produce a conspicuous calling song to attract females for mating (Fig. 1). However, in some parts of the cricket's range a singing male risks also attracting the acoustically orienting parasitoid fly *Ormia ochracea* (Diptera: Tachinidae: Ormiini), which parasitizes *Gryllus* species on the mainland USA (Cede 1975; Walker 1986) and *T. oceanicus* in Hawaii (Zuk *et al.* 1993). Ormiines are unique because they have specialized ears that enable them to locate their hosts by their songs (Robert *et al.* 1992; Allen 1995). A gravid *O. ochracea* female locates a cricket and larviposits on and around it; larvae burrow into the host and develop within the host for 7-10 days before emerging to pupate, killing the host within one day of emergence (Adamo *et al.* 1995a). Although larvae deposited near a male may parasitize female crickets attracted to that male, females have a relatively low parasitoid prevalence compared to males (Zuk *et al.* 1993, Adamo *et al.* 1995b).

Figure 1. Sonogram of a typical *T. oceanicus* calling song.

Because the same calling song produced by male crickets to attract females is used by flies to locate hosts (Cede 1975), Hawaii males face a trade-off between producing elaborate songs to attract females and minimizing singing to avoid attracting the fly. Previous studies of the effects of parasitization on cricket song have been confined to comparisons of species that differ in parasitization; such interspecific comparisons may have confounding effects that have nothing to do with the parasitoid (Rotenberry *et al.* 1996). *T. oceanicus* offers

me the unique opportunity to study the evolution of an acoustic mating display by comparing populations of the same species. Zuk and her colleagues have described *T. oceanicus* populations varying in parasitoid prevalence from 0% to 31% (Zuk *et al.* 1993; Rotenberry *et al.* 1996). These populations have a corresponding variation in calling song structure, suggesting that selection by the parasitoid has played a role in song evolution (Zuk *et al.* 1993; Rotenberry *et al.* 1996).

The long term goal of my research is to determine how natural selection imposed by the parasitoid fly and sexual selection imposed by female crickets interact to shape the evolution of *T. oceanicus* reproductive biology. My research focuses on the following questions:

1) Does *O. ochracea* influence male cricket reproductive success even before the cricket dies?

Ormiine parasitoids significantly reduce host lifespan (*e.g.*, Lehmann and Heller 1997), and my work on *T. oceanicus* indicates that parasitization may also have detrimental fitness consequences prior to host death. *T. oceanicus* males transfer sperm to females in discrete spermatophores. In two separate experiments of spermatophore replacement rates in parasitized and unparasitized males conducted in 1997, parasitized males produced significantly fewer spermatophores than unparasitized males. An examination of mating behavior in 1998 supported the spermatophore replacement studies and showed that parasitized males copulated significantly less frequently than unparasitized males. These results suggest that parasitization reduces male cricket reproductive success, and confirm that the fly is an important selective agent for crickets. This research is ongoing and I plan to address whether the fecundity of females mated to parasitized males is lower than that of females mated to unparasitized males.

2) Do female flies and female crickets prefer the same aspects of male song?

Acoustically-orienting parasitoids are generally more likely to find males with high pulse numbers (*e.g.*, long chirp, Fig. 1) in their songs (Wagner 1996; Lehmann and Heller 1998). Zuk *et al.* (1998) confirmed this by showing that parasitized *T. oceanicus* males within a population had more long chirp and less short chirp components in their songs than unparasitized males. These differences among individuals were apparent even immediately after infestation, suggesting that differences in calling were not due to parasitization,

but rather that flies were more likely to locate a male with a greater proportion of long chirp in his songs (Zuk *et al.* 1998).

If flies prefer the same song structure variables as female crickets, then male crickets may face a compromise between attracting females for mating and also attracting flies (*e.g.*, Wagner 1996). In this case, cricket song may either not change much over evolutionary time because of stabilizing natural and sexual selection pressures, or female cricket choice may be relaxed in the parasitized populations such that directional selection by flies is the predominant force affecting song evolution. Alternatively, if flies differ from female crickets in their song preferences, then cricket song is expected to evolve away from what flies prefer and toward what female crickets prefer. Direct tests of fly preference are required to distinguish between these alternative predictions.

In the summer of 1998 I conducted song broadcasts to test for song preferences of parasitoid flies in Hilo, Hawaii. I broadcasted pairs of songs differing in one variable only, and collected flies attracted to each song. A total of 342 flies were collected over 27 nights. I found that flies significantly preferred songs with many long chirp pulses and few short chirps. In the future I intend to directly test for fly preferences in other parasitized populations, to evaluate the generality of the Hilo results and to determine whether fly preferences vary among populations within the Hawaiian islands. The expectation is that fly preferences will be strongest in Kauai, which has the highest parasitoid prevalence, and weakest in Oahu, which has the lowest parasitoid prevalence (Rotenberry *et al.* 1996).

Neuroethological studies suggest that female crickets generally also prefer the long chirp (Pollack and Hoy 1981), so that female crickets and flies may converge in their song preferences (*e.g.*, Wagner 1996). However, if a female approaches a male whose song has attracted flies, she risks also becoming parasitized. Therefore, it is possible that females are less choosy in populations with high parasitoid prevalence. For example, female crickets respond differently to male songs depending on the perceived risk of predation (Hedrick and Dill 1993; Csada and Neudorf 1995). I will therefore also conduct laboratory experiments to directly test the song preferences of females from populations varying in parasitoid prevalence, to test the hypothesis that females from heavily parasitized populations are less choosy.

## SCIENCE REPORT

3) Does cricket calling activity correlate positively with female cricket attraction and negatively with parasitoid prevalence?

Calling in *T. oceanicus* and other field crickets is energetically expensive (e.g., Hoback and Wagner 1997). Therefore, it is possible that females prefer males who are able to sustain high levels of calling during a night (Walker 1983; Crnokrak and Roff 1998), or that males that call a lot are simply more likely to be calling when a female passes (Zuk and Simmons 1997). The female may then evaluate male quality based on song structure elements such as pulse rate, frequency, and intensity (Pollack and Hoy 1981; Doolan and Pollack 1985). In either case, because calling also attracts flies, calling activity is expected to be negatively correlated with parasitoid prevalence (Cede 1991).

In the summer of 1997 I determined the calling activity of 39 caged males for two to eight consecutive nights in Hilo, Hawaii. Field calling activity was significantly repeatable, which means that a male can be reliably characterized as a high or low caller. Regression analysis showed that calling activity also significantly predicts female cricket attraction. A comparison of calling activity between the Hilo population and an unparasitized *T. oceanicus* population studied by Orsak (1988) revealed that Hilo males call significantly less, supporting the idea that although high calling activity increases the chances of attracting mates, calling activity is reduced in parasitized populations because it also attracts flies. I plan to examine calling activity in the other Hawaiian islands in the future, to examine the question posed above.

4) Do male cricket calling patterns differ among parasitized and unparasitized populations?

In addition to the quantity of calling, when a male calls during the night may have important consequences for his reproductive success. For example, males should peak in calling activity at the same time during the night that receptive females peak in searching activity (Walker, 1983). Orsak (1988) and Loher and Orsak (1985) examined calling patterns in an unparasitized *T. oceanicus* population in Moorea, French Polynesia, and showed that males peak in calling at dusk and dawn. In contrast, parasitized populations of *Gryllus* species have a dawn peak but not a dusk peak; this result has been attributed to selection by the parasitoid fly because flies are more active at dusk than at dawn (French and Cade 1987).

In 1997 I examined the individual calling patterns of 39 male crickets in Hilo and found a pronounced dusk peak but no dawn peak in calling activity. Data from fly captures showed that the calling activity peak coincides with the peak in fly searching activity, so that males do not appear to have shifted calling to avoid flies. I also intend to examine calling patterns in Oahu and Kauai, to determine whether a shift in the timing of calling has occurred in those populations. I am especially interested in the heavily infested Kauai population, where selection by the fly has potentially resulted in crickets calling more at dawn than at dusk.

This research will increase our understanding of how cricket behavior evolves and, more generally, of how conflicting selection pressures interact to produce phenotypes over evolutionary time (e.g., Andersson 1994: 234).

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