

Eavesdropping to Find Mates: The Function of Male Hearing for a Cicada-Hunting Parasitoid Fly, *Emblemasoma erro* (Diptera: Sarcophagidae)

Brian J. Stucky^{1,2,3}

¹Department of Ecology and Evolutionary Biology, University of Colorado, 334 UCB, Boulder, CO, 80309 (stuckyb@colorado.edu)

²Florida Museum of Natural History, University of Florida, 1659 Museum Rd, Gainesville, FL, 32611 (stuckyb@flmnh.ufl.edu), and

³Corresponding author, e-mail: stuckyb@flmnh.ufl.edu

Subject Editor: Michael Heethoff

Received 25 February 2016; Accepted 19 May 2016

Abstract

Females of several species of dipteran parasitoids use long-range hearing to locate hosts for their offspring by eavesdropping on the acoustic mating calls of other insects. Males of these acoustic eavesdropping parasitoids also have physiologically functional ears, but so far, no adaptive function for male hearing has been discovered. I investigated the function of male hearing for the sarcophagid fly *Emblemasoma erro* Aldrich, an acoustic parasitoid of cicadas, by testing the hypothesis that both male and female *E. erro* use hearing to locate potential mates. I found that both male and nongravid female *E. erro* perform phonotaxis to the sounds of calling cicadas, that male flies engage in short-range, mate-finding behavior once they arrive at a sound source, and that encounters between females and males at a sound source can lead to copulation. Thus, cicada calling songs appear to serve as a mate-finding cue for both sexes of *E. erro*. *Emblemasoma erro*'s mate-finding behavior is compared to that of other sarcophagid flies, other acoustic parasitoids, and nonacoustic eavesdropping parasitoids.

Key words: insect hearing, eavesdropping, parasitoid, mating behavior, *Emblemasoma*

At least six species of flies of the tachinid tribe Ormiini (Diptera: Tachinidae) and two species of flies of the sarcophagid genus *Emblemasoma* (sensu Pape 1990; Diptera: Sarcophagidae) are parasitoids with an unusual method of finding their hosts: Female flies have highly sensitive ears that allow them to listen for, and home in on, the airborne acoustic signals of their host crickets, katydids, and cicadas (Cade 1975; Soper et al. 1976; Burk 1982; Fowler and Kochalka 1985; Lakes-Harlan and Heller 1992; Walker 1993; Allen 1998; Stucky 2015). Females perform rapid, positive phonotaxis to the mating calls of their hosts, but all previous studies have found that males are not attracted to these sounds in the field (Fowler 1987; Walker 1993; Farris et al. 2008; Lakes-Harlan et al. 2014). Nevertheless, male acoustic parasitoids also have ears. They possess the same tympanal structures as females, and the males' tympana are physiologically functional (Robert et al. 1992; Lakes-Harlan et al. 2014; Lakes-Harlan and Lehmann 2015). So far, however, no definite adaptive function of male hearing has been demonstrated for any of these fly species.

Here, I present the results of an investigation of the function of male hearing in the sarcophagid parasitoid *Emblemasoma erro* Aldrich. *Emblemasoma erro* is an acoustic eavesdropping parasitoid of the cicada *Neotibicen dorsatus* (Say) (Hemiptera: Cicadidae) in the central Great Plains region of North America, and as with other

sarcophagid and tachinid acoustic parasitoids, females of *E. erro* orient to the mating calls of their hosts for larviposition (Stucky 2015). After informally observing that male *E. erro* were also attracted to the acoustic signals of cicadas, I hypothesized that both male and female *E. erro* might use the calling songs of their hosts as a means for locating potential mates. To test this hypothesis, I investigated the attractiveness of host cicada calls to both male and female *E. erro*, and I tested whether nongravid female *E. erro* also perform phonotaxis to cicada calls, as would be expected if these flies use cicada calls to find mates. I also observed the behaviors of male *E. erro* at a sound source and attempted to observe the mating behavior of *E. erro* in the field. All results suggested that cicada calls serve as mate-finding cues for this parasitoid. I discuss the mate locating behavior of *E. erro* in the context of the mating behaviors of other sarcophagid species, other acoustic parasitoids, and, more broadly, eavesdropping parasitoids in general.

Materials and Methods

Field work for this study was conducted in late July, August, and early September of 2011–2013 at study sites located in Ellsworth,

McPherson, and Reno counties in central Kansas (Fig. 1). The habitat at all study sites was qualitatively similar and consisted of native midgrass prairie vegetation intermixed with both naturally occurring and planted trees.

Phonotaxis by *E. erro* was studied in the field by broadcasting appropriate acoustic stimuli from a loudspeaker, a technique that has been widely used by researchers working on other species of acoustic parasitoids (e.g., Cade 1975; Soper et al. 1976; Lakes-Harlan et al. 2000; Lehmann 2003). The acoustic stimuli were designed to represent the calling song of the host cicada *Neotibicen dorsatus*. Details of the methods used to construct these signals are provided in Stucky (2015). Briefly, the calling songs of 20 different male *N. dorsatus* were recorded and analyzed to determine the values of three acoustic parameters: peak frequency, chirp length, and chirp rate (here, “chirp” is equivalent to the term “pulse group” defined in Stucky (2015); see Cole (2008) for a spectrogram and oscillograms of the *N. dorsatus* calling song). The mean values of these parameters were used to construct representative “model calls” that represented the average mating call of male *N. dorsatus* from the general study area. Model calls were constructed either directly from the recordings of *N. dorsatus* or by generating synthetic signals from amplitude-modulated sine waves. The synthetic signals had a frequency of 5.64 kHz, chirp length of 20.3 ms, and a chirp rate of 37 chirps per second. 5.64 kHz is higher than the observed mean peak frequency of *N. dorsatus* (4.31 kHz), but *E. erro* are much more responsive to signals of 5.64 kHz than 4.31 kHz (B. Stucky, unpublished data), so the higher frequency was used. *Neotibicen dorsatus* has a broadband call with peak acoustic energy from ~3 kHz to 7 kHz (Cole 2008), so the synthetic signals were still broadly representative of the natural calling song.

For direct behavioral observations, sounds were broadcast from a tweeter speaker (Pyle PH44, Pyle Audio Inc., Brooklyn, NY) mounted in the top of a wooden box, and flies were observed as they arrived at the speaker and while they remained on or near the broadcast apparatus. I did not attempt to estimate the numbers of female and male flies that were attracted during these behavioral

observations because flies sometimes depart and return to a sound source multiple times during a broadcast (B. Stucky, personal observation), which makes manually counting flies as they arrive unreliable. Instead, acoustic live traps (Stucky 2016) were used to objectively quantify the comparative phonotactic responsiveness of male and female *E. erro*.

For each trapping session, three traps were deployed at a field site and the synthetic *N. dorsatus* call was simultaneously broadcast from all three traps for 30 min. The traps were arranged linearly on the ground with 10 m between adjacent traps. To provide additional information about *E. erro*'s phonotactic behavior, the relative signal amplitudes among the three traps were generally not the same and differed by as much as 18 dB between the loudest and quietest traps. Because of this, the signals were rotated among the traps every 10 min so that, after 30 min, all three traps had broadcast at all three amplitudes for the same amount of time. After every 10 min of broadcasting, the flies captured by each trap were counted and sexed (i.e., captured flies were counted and sexed before the signals were rotated among the traps and again at the end of the last broadcast). Absolute broadcast amplitudes ranged from 85 to 117 dB SPL (reference 20 μ Pa) at 1 m from the loudspeaker, as measured with a RadioShack model 33-2055 SPL meter (RadioShack Corporation, Fort Worth, TX) set to C-weighting. For comparison, the natural call of male *N. dorsatus*, measured using the same SPL meter, is typically ~100 dB SPL at 0.5 m (B. Stucky, unpublished data). To avoid pseudoreplication, no captured flies were released until after trapping was completed at a location. Traps were only operated in the afternoons when the host cicadas were naturally active. Trapping in 2011 was part of a larger study of *E. erro*'s phonotactic behavior, the full results of which will be reported in a separate paper.

To test whether nongravid female flies (defined here as females with no live first-instar larvae in their incubatory pouches) perform positive phonotaxis to host calls, I dissected the abdomens of 20 female flies that were captured at broadcasts of the *N. dorsatus* calling song and noted the presence or absence of larvae. In addition, in 2012 I tested the phonotactic responses of two female flies that had

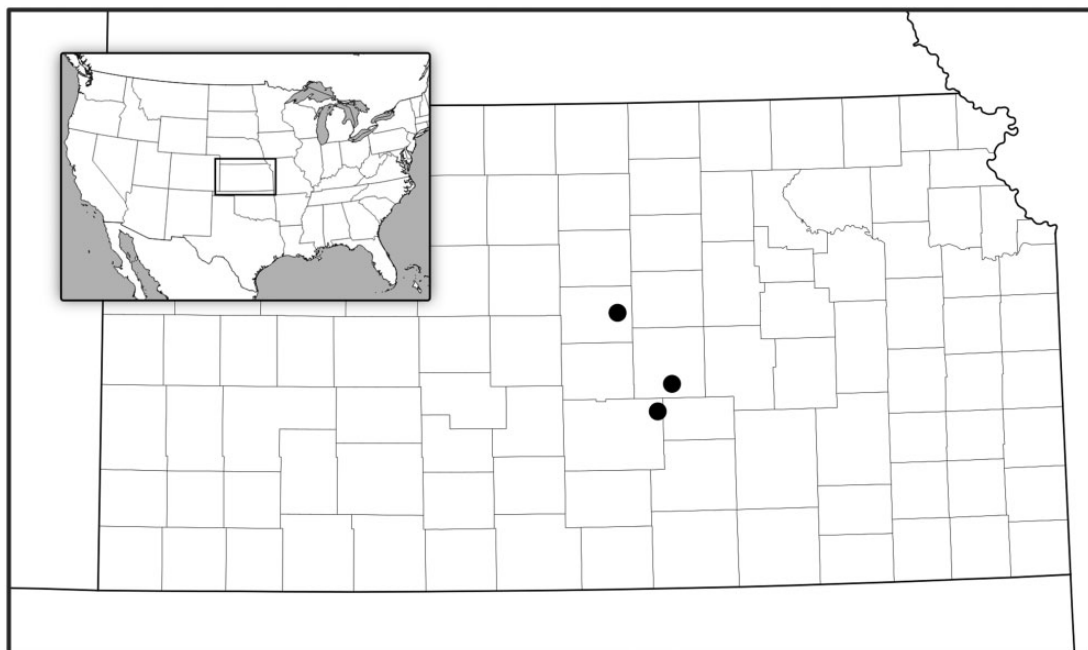


Fig. 1. Locations of study sites for the acoustic trapping experiments. The inset map indicates the location of the main map in the United States.

been reared from infected *N. dorsatus* collected in the field. Neither fly had previously been exposed to either male flies or cicadas. Each fly was tested separately. For each test, the flies were released into a large, outdoor, rectangular screen cage (~1.8 m wide on each side and 2.1 m high in the center) and given several minutes to acclimate to the enclosure. A portable digital audio player (Samsung Galaxy Player 4.0) was held on the side of the cage opposite to the side on which the fly was perched, and the model call of *N. dorsatus* was broadcast from the audio player's onboard speaker. Depending on the location of the fly, the distance between the fly and speaker at the start of the broadcast varied between ~1.8 and 3.1 m. Playback was terminated once a fly performed complete phonotaxis to the speaker or after ~2 min if the fly did not travel to the sound source. The playback procedure was repeated up to 4 times for each fly.

The overall proportion of male flies captured by the acoustic traps across all years and study sites was analyzed using an exact binomial test. To further investigate the comparative phonotactic behaviors of female and male flies, the numbers of flies arriving at the call broadcasts were analyzed using Poisson regression (i.e., generalized linear models with log link function and Poisson-distributed response) (Dobson and Barnett 2008). The predictor variable of primary interest was fly *sex*, but *field site*, *year*, and relative *amplitude* were also considered as predictors. To account for possible variations in male and female responses across the study conditions, the pairwise interactions of fly *sex* with each of *field site*, *year*, and *amplitude* were also evaluated. The effect of each explanatory variable was tested by comparing a reduced model against the full model using the difference of their deviance statistics (i.e., likelihood ratio tests) (Dobson and Barnett 2008). Confidence intervals (CI) for the overall estimated proportions of males and nongravid females arriving at call broadcasts were calculated using the Wilson method (also known as the score confidence interval) (Wilson 1927; Agresti and Coull 1998). All statistical analyses were done using R version 3.1.3 (R Core Team 2015).

Results

Phonotaxis by Male Flies

Traps broadcasting the model *N. dorsatus* call were operated at three field sites for a total of 24 trap-hours and captured a total of 110 *Emblemasoma erro* (Table 1). Of these, 76 (69.1%) were female and 34 (30.9%) were male. Considering all trapping data together, significantly more females than males were captured by the traps (exact binomial test: $P < 0.001$; 95% CI for the proportion of male flies: 0.230–0.401).

The results of the Poisson regression analysis of the numbers of flies captured in the acoustic traps are given in Table 2. As expected from the binomial test of the aggregated data, there were significant differences in the numbers of male and female flies that were captured ($P < 0.001$), but the proportions of males and females also varied among the study years (interaction of fly *sex* and *year*: $P = 0.0177$). The proportion of male flies captured in 2013 was

Table 1. Total numbers of female and male *E. erro* captured in acoustic traps for each study year

Year	Female	Male	Total
2011	22	9	31
2012	36	7	43
2013	18	18	36
Total	76	34	110

much higher than in 2011 and 2012 (Table 1); there was no obvious reason for this pattern. There were no differences in the proportions of males and females trapped among the field sites (interaction of fly *sex* and *field site*: $P = 0.369$). Signal amplitude had a strong effect on the number of flies captured by a trap ($P < 0.001$), but amplitude had no effect on the proportions of male and female flies that were trapped (interaction of *amplitude* and fly *sex*: $P = 0.386$). Because broadcast amplitude had no effect on the relative phonotactic responses of male and female *E. erro*, the effect of amplitude on fly phonotaxis is not considered further here and will instead be analyzed as part of a separate paper addressing acoustic signal perception by *E. erro*.

On three occasions, an individual trap only caught male *E. erro*. No flies were ever captured by the traps when the loudspeakers were not broadcasting.

Attraction of male flies was not just an artifact of the broadcast apparatus. Male flies were also occasionally captured in the field on the outside of mesh cages housing calling male *N. dorsatus* cicadas, which confirmed that they perform phonotaxis to the natural mating calls of male cicadas as well as to the loudspeakers.

Phonotaxis by Nongravid Female Flies

Twenty female flies were collected at model *N. dorsatus* call broadcasts and dissected to determine whether they were gravid (i.e., whether they contained first-instar larvae). Of these 20 flies, 6 (30%) had no larvae in their incubatory pouches and 14 (70%) contained first-instar larvae (95% CI for the proportion of nongravid females: 0.145–0.519). The six nongravid flies all contained eggs only. In some cases, the eggs were quite small and clearly at an early point in their development. Collection dates ranged from late July to early September; however, because *E. erro* is multivoltine in the central Great Plains (Stucky 2015), collection date is not a reliable predictor of fly age. Regardless, it was clear that none of the nongravid females had exhausted their egg supply.

In the tests of the phonotactic responses of the two reared female *E. erro* that had not been exposed to either male flies or potential hosts, both flies performed complete flight phonotaxis to the broadcast speaker. The first fly was tested 3 times, and it traversed the width of the cage to arrive at the speaker in the first two tests. For the third test, the fly did not travel to the speaker, but the broadcast still appeared to trigger walking about the wall of the cage and several short flights. The second fly was tested 4 times, and performed complete flight phonotaxis to the speaker all 4 times. Neither fly showed any obvious response to the speaker when it was not broadcasting the model *N. dorsatus* call.

Table 2. Analysis of deviance table for the Poisson regression model of the number of flies captured in the acoustic traps

Variable	Deviance (χ^2)	d.f.	P
<i>Amplitude</i>	124.325	1	<0.001
<i>Sex</i>	16.451	1	<0.001
<i>Year</i>	3.297	2	0.192
<i>Field site</i>	0.215	2	0.898
<i>Sex</i> × <i>year</i>	8.071	2	0.0177
<i>Sex</i> × <i>field site</i>	1.993	2	0.369
<i>Sex</i> × <i>amplitude</i>	0.751	1	0.386

Significance values for individual predictor variables were calculated using "type II" tests as implemented in the "car" package for R (Fox and Weisberg 2011).

Behavioral Observations

Male *E. erro* that were attracted by the broadcast loudspeaker typically either perched on the top of the loudspeaker box or immediately pursued one or more flies that had previously arrived at the loudspeaker. When another fly was visually detected by a male, the male would often rapidly approach the second fly either on foot or in the air and make physical contact with it. Such contact generally appeared to be an attempt at copulation, because the pursuing male would grasp the second fly and mount it in the coupling position typical of many Diptera (McAlpine 1981). Male flies attempted to mount both males and females and seemed unable to discriminate between the sexes prior to making physical contact. When a male attempted to mount another fly, it usually resulted in both flies departing from the loudspeaker box, so it was rarely possible to determine whether attempted couplings were ultimately successful.

During these and other field experiments with *E. erro*, I observed three apparently successful matings between flies that had been attracted to model cicada call broadcasts. Two matings involved male and female flies that were observed copulating inside one of the live traps after both had been captured. The durations of these matings were not precisely timed, but in the second case, the pair remained together for at least 25 min. In the third observation of mating in the field, two flies that landed near the loudspeaker began copulating, then flew off joined together. Attempts were also made to observe mating behavior in captivity in the lab, but these efforts were mostly unsuccessful. However, putative male mating behavior in captivity was similar to that observed at the sound broadcasts in the field, with males pursuing potential mates either by walking or by flight. Only one successful mating was observed in captivity, between a pair of flies that had been reared from a parasitized *N. dorsatus* (Fig. 2). These flies remained in copula for at least 90 min.

Discussion

All results of this study were consistent with the hypothesis that *Emblemasoma erro* uses the acoustic sexual signals of its hosts as a means for locating potential mates. In the field, both male flies and non gravid female flies performed positive phonotaxis to acoustic stimuli mimicking the calls of their host cicadas. Unmated female flies with no previous exposure to male flies or host signals were also phonotactically responsive. Once male flies arrived at a sound source, they pursued and tried to mate with other flies that were also attracted to the acoustic stimulus. Although it was not known with certainty whether the non gravid female flies captured in this study were seeking mating opportunities, these flies were obviously incapable of parasitizing hosts, and the observation of three mating pairs in the field indicates that at least some sexually receptive females perform phonotaxis to cicada calls. Traveling to calling cicadas is an expenditure of both time and energy, and it is difficult to imagine any other compensatory benefit to either males or non gravid females besides finding mates.

This study cannot rule out the possibility that female *E. erro* also play a role in attracting males for mating (e.g., with a pheromone signal), but it seems unlikely. Observations of male *E. erro* suggest that even at very close range, they cannot easily discriminate between receptive females and other females and males. Indeed, their approach to finding a suitable female appears to be mostly trial and error, as has been observed for some other sarcophagid species (Thomas 1950; Sharma 1975; Adham et al. 1980). In any case, the acoustic stimulus by itself is clearly sufficient to attract male flies. On three occasions, only male *E. erro* were captured by an acoustic



Fig. 2. Mating pair of *Emblemasoma erro*.

trap, and at the beginning of a call broadcast, it was not uncommon for one or more male flies to arrive before any females.

There is remarkably little information available about the mate-finding behaviors of other sarcophagids. The literature does suggest, though, that there are two main strategies used by these flies for locating mates. In the first strategy, male flies aggregate at visual markers that are unrelated to adult or larval food resources, such as the tops of hills, and females visit these locations to mate (Chapman 1954; Dodge and Seago 1954; Povolný and Verves 1997). This behavior, often referred to as “hilltopping”, is common among many species of calyptrate flies (Chapman 1954; Dodge and Seago 1954; Alcock and Schaefer 1983). In the second strategy, both males and females travel to adult feeding sites or larviposition sites to seek mates. This has been observed, for example, in sarcophagid species that feed on dung and carrion (Thomas 1950; Martín-Vega and Baz 2013; Rivers and Dahlem 2013). Males of at least one species, *Sarcophaga bullata* Parker, also produce a pheromone that is attractive to females (Girard and Budris 1975; Girard et al. 1979).

The mate-finding behavior of *E. erro* appears to be a highly specialized version of the second sarcophagid mate finding strategy described in the previous paragraph. Both males and females are attracted to larviposition sites (i.e., male cicadas) to find mates, and both sexes use cicadas’ mating calls as the cue for locating these sites. The two mate-finding strategies used by sarcophagids are not mutually exclusive, of course, so it is entirely possible that *E. erro* males also aggregate at visual markers. The ability to facultatively switch strategies could be especially advantageous at times when hosts are not abundant, such as early in the season.

Once they arrive at a calling cicada, the mating behaviors of male *E. erro* are similar to other members of their family. Although sarcophagid species vary in their strategies for initially bringing the sexes together, at close range, most sarcophagid mating systems seem to depend on males that actively search for females visually and, once a potential mate is spotted, attempt to intercept the female

and initiate mating with little or no courtship behavior (Thomas 1950; Moradeshaghi and Bohart 1968; Sharma 1975; Adham et al. 1980; Spofford and Kurczewski 1985; Alcock 2000; Gilbert and Kim 2007; see Spofford and Kurczewski 1985; for an exception). Several authors have commented on the apparent inability of male sarcophagids to discriminate among receptive females, unreceptive females, other males, or even other species (Thomas 1950; Sharma 1975; Adham et al. 1980).

Only ~30% of the flies captured in the live traps were male, but this might underestimate the true proportion of males that were attracted to the sound broadcasts. During trap operation, males could often be seen perching on the outside of the trap, from where they would watch for and attempt to intercept other flies that arrived. These males usually did not enter the trap and they sometimes persisted on the outside of the trap until the broadcast terminated. Carrion-feeding sarcophagid species in which both males and females are attracted to carcasses to seek mates can be caught with carrion-baited live traps, and, in at least one study, the percentage of males captured in this way was very similar to that observed here for *E. erro* (Martín-Vega and Baz 2013). In that study, male carrion-feeding flies that were attracted to the carrion-baited traps stationed themselves near the food resource to intercept mates and did not always enter the traps (Martín-Vega and Baz 2013), much like the behavior of *E. erro* males at the acoustic traps.

Among the species of acoustic parasitoids that have been studied so far, *E. erro* is the only one for which there is strong evidence that hearing plays a significant role in the lives of the adult males. Yet males of all species appear to have physiologically functional ears (Lakes-Harlan and Lehmann 2015), so why have other acoustic parasitoids not evolved a similar strategy to locate mates? For tachinid acoustic parasitoids of the tribe Ormiini, the answer might lie with the biology of their hosts. As far as is known, these flies all parasitize crickets or katydids (Orthoptera: Ensifera) that produce their calling songs at night (Lehmann 2003). Thus, female ormiines must search for their hosts nocturnally. However, like sarcophagids, males of many tachinid species depend on vision for short-range mate finding (Wood 1987), and this requirement might preclude them from using nocturnal host calls as long-range mate finding cues. Indeed, there is evidence that some ormiines use hilltopping to locate mates (Lederhouse et al. 1976; Burk 1982). Also, several authors have posited that the ormiine ear might function to evade bat predation (Robert et al. 1992, 1996), and while there is experimental evidence supporting this hypothesis for females of one species, *Ormia ochracea* (Bigot) (Rosen et al. 2009), the behavioral response of males to bat ultrasound has not been reported.

There are no obvious explanations for the absence of acoustic mate finding in *Emblemasoma auditrix* (Shewell), the only other species of *Emblemasoma* for which any detailed life history information is available. As with *E. erro*, female *E. auditrix* hunt for host cicadas acoustically, and the host cicadas for both species are active during the day (Soper et al. 1976; Lakes-Harlan et al. 2000). Despite thorough investigation of multiple hypotheses, including the use of host signals to find mates, Lakes-Harlan et al. (2014) were unable to identify any adaptive function for hearing in male *E. auditrix*. The mating system of *E. auditrix* is not well understood, but it appears to be a variant of hilltopping behavior in which males aggregate in patches of vegetation and use visual cues to pursue potential mates (Lakes-Harlan et al. 2014).

Although they both host on cicadas, *E. auditrix* and *E. erro* are in several respects quite different from one another. *Emblemasoma auditrix* is highly specialized and only attacks a single cicada species, *Okanagana rimosa* (Say) (Lakes-Harlan et al. 2000). *Emblemasoma*

erro, on the other hand, has a broader host range, and its hosts usually have a considerably longer seasonal presence than *O. rimosa* (B. Stucky, in preparation). *Emblemasoma auditrix* is univoltine while *E. erro* in the central Great Plains is multivoltine (Stucky 2015). It seems plausible that these contrasting natural history traits could favor one mate finding strategy over another, but the extent to which they, or other factors, might have influenced the evolution of these flies' mating systems is not known.

Emblemasoma erro's use of its hosts' communication signals as a mate-finding cue appears to be unique among the few well-studied species of acoustic parasitoids, but there is convincing evidence that some species of nonacoustic eavesdropping parasitoids also use this strategy. At least four species of tachinid flies [*Euclytia flava* (Townsend), *Gymnosoma rotundatum* (Linnaeus), *Hemyda aurata* Robineau-Desvoidy, and *Trichopoda pemipēs* (Fabricius)] and one species of phorid fly (*Apocephalus paraponerae* Borgmeier) eavesdrop on the pheromone signals of other insects to locate both potential hosts and potential mates (Mitchell and Mau 1971; Harris and Todd 1980; Aldrich 1985; Feener et al. 1996; Jang and Park 2010; Higaki and Adachi 2011). (It is not entirely clear, however, whether host finding by *A. paraponerae* is a case of true eavesdropping (Hermann et al. 1984; Feener et al. 1996)). Some parasitoid wasps that eavesdrop on pheromones have also adopted this strategy, such as the pteromalid *Tomicobia tibialis* Ashmead (Bedard 1965; Rice 1969). A few other cases in which male eavesdropping parasitoids have been attracted to host pheromones have also been reported, but without direct observation of mating or sexual behaviors following chemotaxis (Kennedy 1979, 1984; Dixon and Payne 1980; Zaki 1985; Micha and Wyss 1996; Gabryś et al. 1997; Aldrich et al. 2006; Benelli et al. 2014). In some studies, male behavior is difficult to interpret because it is not always clear if the host signal by itself is attractive to males or if females that arrive at the signal source are subsequently responsible for attracting males. Regardless, *E. erro* is clearly not alone in its use of host communication signals as a cue for locating potential mates.

Every summer, the grasslands of the central Great Plains ring with the mating calls of male *Neotibicen dorsatus* trying to attract female cicadas. By producing their calls, these male cicadas unwittingly betray their locations to female *Emblemasoma erro* searching for hosts for their offspring. This study reveals that the acoustic signals of *N. dorsatus* serve yet another purpose in *E. erro*'s life cycle. For these flies, the call of *N. dorsatus* is also a "love song" that both male and female *E. erro* exploit as a means for finding mating opportunities. *Emblemasoma erro* and olfactory eavesdroppers with analogous mate-finding behaviors demonstrate that for at least some eavesdropping parasitoids, insect communication signals do not merely provide an efficient way to find potential hosts—they provide an efficient way for these parasitoids to find each other, too.

Acknowledgments

I thank the private landowners who allowed me access to their property for this study, as well as the Kansas Department of Wildlife, Parks, and Tourism for providing access to state-managed lands. I am very grateful to Bruce and Pat Stucky, Erin Stucky, and Rob Guralnick for providing invaluable and enthusiastic assistance in the field. I also thank Rob Guralnick, Erin Stucky, and three anonymous reviewers for their insightful feedback on earlier versions of the manuscript. This work was funded in part by research grants from the Department of Ecology and Evolutionary Biology at the University of Colorado, the University of Colorado Museum of Natural History, and a Sigma Xi Grants-in-Aid of Research award.

References Cited

- Adham, F. K., N. Z. Zohdy, and M. A. Yeramian. 1980. Studies on the mating behaviour of the flesh fly *Parasarcophaga argyrostoma* (Robineau-Desvoidy) (Diptera: Sarcophagidae). *J. Egypt. Soc. Parasitol.* 10: 349–357.
- Agresti, A., and B. A. Coull. 1998. Approximate is better than “exact” for interval estimation of binomial proportions. *Am. Stat.* 52: 119.
- Alcock, J. 2000. The natural history of a miltogrammine fly, *Miltogramma rectangularis* (Diptera: Sarcophagidae). *J. Kans. Entomol. Soc.* 73: 208–219.
- Alcock, J., and J. E. Schaefer. 1983. Hilltop territoriality in a Sonoran desert bot fly (Diptera: Cuterebridae). *Anim. Behav.* 31: 518.
- Aldrich, J. R. 1985. Pheromone of a true bug (Hemiptera-Heteroptera): attractant for the predator, *Podisus maculiventris*, and kairomonal effects, pp. 95–119. *In* T.E. Acree D.M. Soderlund (eds.), *Semiochemistry flavors pheromones*. W. de Gruyter, Berlin, New York.
- Aldrich, J. R., Khrimian, A. A. Zhang, and P. W. Shearer. 2006. Bug pheromones (Hemiptera: Heteroptera) and tachinid fly host-finding. *Denisia* 19: 1015–1031.
- Allen, G. R. 1998. Diel calling activity and field survival of the bushcricket, *Sciarasaga quadrata* (Orthoptera: Tettigoniidae): a role for sound-locating parasitic flies? *Ethology* 104: 645–660.
- Bedard, W. D. 1965. The biology of *Tomicobia tibialis* (Hymenoptera: Pteromalidae) parasitizing *Ips confusus* (Coleoptera: Scolytidae) in California. *Contrib. Boyce Thompson Inst. Plant Res.* 23: 77–81.
- Benelli, G., A. Carpita, S. Simoncini, A. Raspi, and A. Canale. 2014. For sex and more: attraction of the tephritid parasitoid *Psytalia concolor* (Hymenoptera: Braconidae) to male sex pheromone of the olive fruit fly, *Bactrocera oleae*. *J. Pest Sci.* 87: 449–457.
- Burk, T. 1982. Evolutionary significance of predation on sexually signalling males. *Fla. Entomol.* 65: 90–104.
- Cade, W. H. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* 190: 1312–1313.
- Chapman, J. A. 1954. Studies on summit-frequenting insects in western Montana. *Ecology* 35: 41.
- Cole, J. A. 2008. A new cryptic species of cicada resembling *Tibicen dorsatus* revealed by calling song (Hemiptera: Auchenorrhyncha: Cicadidae). *Ann. Entomol. Soc. Am.* 101: 815–823.
- Dixon, W. N., and T. L. Payne. 1980. Attraction of entomophagous and associate insects of the southern pine beetle to beetle- and host tree-produced volatiles. *J. Ga. Entomol. Soc.* 15: 378–389.
- Dobson, A. J., and A. G. Barnett. 2008. An introduction to generalized linear models, 3rd ed. Chapman & Hall/CRC Texts in Statistical Science Series, CRC Press, Boca Raton.
- Dodge, H. R., and J. M. Seago. 1954. Sarcophagidae and other Diptera taken by trap and net on Georgia mountain summits in 1952. *Ecology* 35: 50.
- Farris, H. E., M. L. Oshinsky, T. G. Forrest, and R. R. Hoy. 2008. Auditory sensitivity of an acoustic parasitoid (*Emblemasoma* sp., Sarcophagidae, Diptera) and the calling behavior of potential hosts. *Brain Behav. E.* 72: 16–26.
- Feener, D. H., Jr, L. F. Jacobs, and J. O. Schmidt. 1996. Specialized parasitoid attracted to a pheromone of ants. *Anim. Behav.* 51: 61–66.
- Fowler, H. G. 1987. Field behavior of *Euphasiopteryx depleta* (Diptera: Tachinidae): phonotactically orienting parasitoids of mole crickets (Orthoptera: Gryllotalpidae: *Scapteriscus*). *J. N. Y. Entomol. Soc.* 95: 474–480.
- Fowler, H. G., and J. N. Kochalka. 1985. Scientific notes: new record of *Euphasiopteryx depleta* (Diptera: Tachinidae) from Paraguay: attraction to broadcast calls of *Scapteriscus acletus* (Orthoptera: Gryllotalpidae). *Fla. Entomol.* 68: 225–226.
- Fox, J., and S. Weisberg. 2011. An R companion to applied regression, 2nd ed. SAGE Publications, Thousand Oaks, Calif.
- Gabryś, B. J., H. J. Gadowski, Z. Klukowski, J. A. Pickett, G. T. Sobota, L. J. Wadhams, and C. M. Woodcock. 1997. Sex pheromone of cabbage aphid *Brevicoryne brassicae*: identification and field trapping of male aphids and parasitoids. *J. Chem. Ecol.* 23: 1881–1890.
- Gilbert, C., and M. P. Kim. 2007. Effects of male age and cervical proprioceptors on sexual aerial pursuit by male flesh flies, *Neobellieria bullata* (Diptera: Sarcophagidae). *J. Insect Behav.* 20: 427–435.
- Girard, J. E., and J. P. Budris. 1975. Sex pheromone in the flesh fly, *Sarcophaga bullata*. *Melsheimer Entomol. Ser.* 20: 1–5.
- Girard, J. E., F. J. Germino, J. P. Budris, R. A. Vita, and M. P. Garrity. 1979. Pheromone of the male flesh fly, *Sarcophaga bullata*. *J. Chem. Ecol.* 5: 125–130.
- Harris, V. E., and J. W. Todd. 1980. Male-mediated aggregation of male, female and 5th-instar southern green stink bugs and concomitant attraction of a tachinid parasite, *Trichopoda pennipes*. *Entomol. Exp. Appl.* 27: 117–126.
- Hermann, H. R., M. S. Blum, J. W. Wheeler, W. L. Overall, J. O. Schmidt, and J. T. Chao. 1984. Comparative Anatomy and Chemistry of the Venom Apparatus and Mandibular Glands in *Dinoponera grandis* (Guérin) and *Paraponera clavata* (F.) (Hymenoptera: Formicidae: Ponerinae). *Ann. Entomol. Soc. Am.* 77: 272–279.
- Higaki, M., and I. Adachi. 2011. Response of a parasitoid fly, *Gymnosoma rotundatum* (Linnaeus) (Diptera: Tachinidae) to the aggregation pheromone of *Plautia stali* Scott (Hemiptera: Pentatomidae) and its parasitism of hosts under field conditions. *Biol. Control* 58: 215–221.
- Jang, S. A., and C. G. Park. 2010. *Gymnosoma rotundatum* (Diptera: Tachinidae) attracted to the aggregation pheromone of *Plautia stali* (Hemiptera: Pentatomidae). *J. Asia Pac. Entomol.* 13: 73–75.
- Kennedy, B. H. 1979. The effect of multilure on parasites of the European elm bark beetle, *Scolytus multistriatus*. *Bull. Entomol. Soc. Am.* 25: 116–118.
- Kennedy, B. H. 1984. Effect of multilure and its components on parasites of *Scolytus multistriatus* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 10: 373–385.
- Lakes-Harlan, R., T. deVries, H. Stöling, and A. Stumpner. 2014. Useless hearing in male *Emblemasoma auditrix* (Diptera, Sarcophagidae) – a case of intralocus sexual conflict during evolution of a complex sense organ? *PLoS ONE.* 9: e87211.
- Lakes-Harlan, R., and K. G. Heller. 1992. Ultrasound-sensitive ears in a parasitoid fly. *Naturwissenschaften* 79: 224–226.
- Lakes-Harlan, R., and G. U. C. Lehmann. 2015. Parasitoid flies exploiting acoustic communication of insects—comparative aspects of independent functional adaptations. *J. Comp. Physiol. A.* 201: 123–132.
- Lakes-Harlan, R., H. Stöling, and T. E. Moore. 2000. Phonotactic behaviour of a parasitoid fly (*Emblemasoma auditrix*, Diptera, Sarcophagidae) in response to the calling song of its host cicada (*Okanagana rimosa*, Homoptera, Cicadidae). *Zoology* 103: 31–39.
- Lederhouse, R. C., R. A. Morse, J. T. Ambrose, D. M. Burgett, W. E. Conner, L. Edwards, R. D. Fell, R. Rutowski, and M. Turell. 1976. Crepuscular mating aggregations in certain *Ormia* and *Sitophaga*. *Ann. Entomol. Soc. Am.* 69: 656–658.
- Lehmann, G. U. C. 2003. Review of biogeography, host range and evolution of acoustic hunting in Ormiini (Insecta, Diptera, Tachinidae), parasitoids of night-calling bushcrickets and crickets (Insecta, Orthoptera, Ensifera). *Zool. Anz. J. Comp. Zool.* 242: 107–120.
- Martín-Vega, D., and A. Baz. 2013. Sex-biased captures of sarcosaprophagous diptera in carrion-baited traps. *J. Insect Sci.* 13: 1–12.
- McAlpine, J. F. 1981. Morphology and terminology – adults, pp. 9–63. *In* J.F. McAlpine, B.V., Peterson, G.E., Shewell, H.J., Teskey, J.R., Vockeroth, and D.M., Wood (eds.), *Man. nearctic dipteral*, vol. 1. Canadian Government Publishing Centre, Hull, Quebec, Canada.
- Micha, S. G., and U. Wyss. 1996. Aphid alarm pheromone (E)- β -farnesene: a host finding kairomone for the aphid primary parasitoid *Aphidius uzbeckistanicus* (Hymenoptera: Aphidiinae). *Chemoecology* 7: 132–139.
- Mitchell, W. C., and R. F. L. Mau. 1971. Response of the female southern green stink bug and its parasite, *Trichopoda pennipes*, to male stink bug pheromones. *J. Econ. Entomol.* 64: 856–859.
- Moradshaghi, M. J., and G. E. Bohart. 1968. The biology of *Euphytomima nomiivora* (Diptera: Sarcophagidae), a parasite of the alkali bee, *Nomia melanderi* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* 41: 456–473.
- Pape, T. 1990. Revisionary notes on American Sarcophaginae (Diptera: Sarcophagidae). *Tijdschr. Voor Entomol.* 133: 43–74.
- Povolný, D., and Y. Verves. 1997. The Flesh-Flies of Central Europe (Insecta, Diptera, Sarcophagidae), Spixiana: Zeitschrift für Zoologie, Supplements. Verlag Dr. F. Pfeil, München, FRG.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing. <http://www.R-project.org>.

- Rice, R. E. 1969. Response of some predators and parasites of *Ips confusus* (LeC.) (Coleoptera: Scolytidae) to olfactory attractants. Contrib. Boyce Thompson Inst. Plant Res. 24: 189–194.
- Rivers, D., and G. Dahlem. 2013. The science of forensic entomology. John Wiley & Sons, Hoboken, NJ.
- Robert, D., J. Amoroso, and R. Hoy. 1992. The evolutionary convergence of hearing in a parasitoid fly and its cricket host. Science 258: 1135–1137.
- Robert, D., R. S. Edgecomb, M. P. Read, and R. R. Hoy. 1996. Tympanal hearing in tachinid flies (Diptera, Tachinidae, Ormiini): the comparative morphology of an innovation. Cell Tissue Res. 284: 435–448.
- Rosen, M. J., E. C. Levin, and R. R. Hoy. 2009. The cost of assuming the life history of a host: acoustic startle in the parasitoid fly *Ormia ochracea*. J. Exp. Biol. 212: 4056–4064.
- Sharma, S. K. 1975. Some observations on the mating behaviour of flesh fly, *Sarcophaga bravicornis* [sic]. Z. Für Angew. Zool. 62: 35–38.
- Soper, R. S., G. E. Shewell, and D. Tyrrell. 1976. *Colcondamyia auditrix* nov. sp. (Diptera: Sarcophagidae), a parasite which is attracted by the mating song of its host, *Okanagana rimosa* (Homoptera: Cicadidae). Can. Entomol. 108: 61–68.
- Spofford, M. G., and F. E. Kurczewski. 1985. Courtship and mating behavior of *Phrosinella aurifacies* Downes (Diptera: Sarcophagidae: Miltogramminae). Proc. Entomol. Soc. Wash. 87: 273–282.
- Stucky, B. J. 2015. Infection behavior, life history, and host parasitism rates of *Emblemasoma erro* (Diptera: Sarcophagidae), an acoustically hunting parasitoid of the cicada *Tibicen dorsatus* (Hemiptera: Cicadidae). Zool. Stud. 54: 17.
- Stucky, B. J. 2016. A new live trap for the acoustically orienting parasitoid fly *Emblemasoma erro* (Diptera: Sarcophagidae). Fla. Entomol. (in press).
- Thomas, H. T. 1950. Field notes on the mating habits of *Sarcophaga* Meigen (Diptera). Proc. R. Entomol. Soc. Lond. Ser. Gen. Entomol. 25: 93–98.
- Walker, T. J. 1993. Phonotaxis in female *Ormia ochracea* (Diptera: Tachinidae), a parasitoid of field crickets. J. Insect Behav. 6: 389–410.
- Wilson, E. B. 1927. Probable inference, the law of succession, and statistical inference. J. Am. Stat. Assoc. 22: 209.
- Wood, D. M. 1987. Tachinidae, pp. 1193–1269. In J.F. McAlpine, B.V. Peterson, G.E., Shewell, H.J., Teskey, J.R., Vockeroth, and D.M., Wood (eds.), Man. nearctic dipteral, vol. 2. Canadian Government Publishing Centre, Hull, Quebec, Canada.
- Zaki, F. N. 1985. Reactions of the egg parasitoid *Trichogramma evanescens* Westw. to certain insect sex pheromones. Z. Für Angew. Entomol. 99: 448–453.