

# Host preferences in a phonotactic parasitoid of field crickets: the relative importance of host song characters

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**Abstract.** 1. Predators, including insect parasitoids, often eavesdrop on prey signals, and as a result, predation can have important effects on the evolution of prey signalling behaviour.

2. The phonotactic parasitoid fly, *Ormia ochracea*, uses the calling songs of male field crickets to locate their field crickets hosts. In the western USA, this fly parasitises the variable field cricket, *Gryllus lineaticeps*. Previous work with one fly population suggested that female flies, like female field crickets, preferentially orient to male songs with higher chirp rates and longer chirp durations, although a limited range of male song types was used in this previous study. The current study, with a different fly population, used field-based, two-speaker choice tests to examine: (1) the effect of male chirp rate and chirp duration on fly attraction, using a natural range of song types; and (2) the relative importance of these song types in host selection by the flies.

3. Three lines of evidence suggested that chirp rate is more important than chirp duration in host selection. (a) The flies consistently preferred higher chirp rates but only sometimes preferred longer chirp durations. (b) The flies consistently preferred higher chirp rate/shorter chirp duration songs to lower chirp rate/longer chirp duration songs. (c) Preferences for longer chirp durations could be eliminated by increasing the amplitude of the less attractive song type, while preferences for higher chirp rates could only sometimes be eliminated by increasing the amplitude of the less attractive song type.

4. Fly predation may favour lower chirp rates and shorter chirp durations in *G. lineaticeps*, and may have resulted in stronger selection on chirp rate than on chirp duration.

**Key words.** Calling song, eavesdropping, field cricket, *Gryllus lineaticeps*, host preference, *Ormia ochracea*, parasitoid.

## Introduction

Predators commonly locate prey using the signals that these prey produce for their own intraspecific communication (reviewed by Zuk & Kolluru, 1998). Eavesdropping by predators on prey signals presumably allows predators to reduce their search costs, and it is known to occur for nearly all types of prey signals, including acoustic (Cade, 1975; Tuttle & Ryan, 1981), visual (Lloyd, 1973; Endler, 1980), and chemical (Mitchell & Mau, 1971; Noldus *et al.*, 1991) signals. Predators not only ex-

plot prey signals, but also often prefer to approach some signal variants to others (Ryan *et al.*, 1982; Wagner, 1996). The reasons that predators express these preference for some prey signal types is usually not clear, but include differences in the ease of localisation, difference in prey vulnerability and differences in prey profitability. Because predators differentially attack males with some signal types, predation can have important effects on the evolution of the signals that animals use for intraspecific communication (e.g. Endler, 1982).

Phonotactic parasitoids have been an important model for studies of predator eavesdropping, particularly the ormiine flies (Tachinidae, Ormiini) that attack bushcrickets and field crickets (reviewed by: Zuk & Kolluru, 1998; Lehmann, 2003). One of the best-studied ormiines is *Ormia ochracea*. In North America

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and Hawaii, female *O. ochracea* are known to attack at least six species of field crickets, including *Gryllus texensis* (Cade, 1975), *G. rubens* (Walker, 1986), *G. firmus* (Walker & Wineriter, 1991), *G. lineaticeps* (Wagner, 1996), *G. integer* (Hedrick & Kortet, 2006) and *Teleogryllus oceanicus* (Zuk *et al.*, 1993). The flies locate their field cricket hosts by orienting to the calling songs of males (Cade, 1975). Once a host has been located, females deposit between one and five first-instar larvae on the prey and approximately six larvae on the ground around the prey (Cade, 1975; Adamo *et al.*, 1995b). Larvae deposited on a cricket, or larvae that make contact with a cricket, burrow into the host through inter-segmental membranes. The larvae first inhabit the flight muscles for 3 days before migrating to the abdomen (life cycle described by Adamo *et al.*, 1995a). Within the abdomen, the larvae feed on the fat body, abdominal muscles and thoracic muscles. The larvae then emerge and pupate 7–10 days after entering a cricket, resulting in the cricket's death within a few days. *Ormia ochracea* not only use field cricket songs to locate their hosts, but also express preferences based on host song, preferentially orienting to some song types over others (Wagner, 1996; Zuk *et al.*, 1998; Gray & Cade, 1999). These song preferences in the flies appear to have affected the evolution of field cricket singing behaviour in *T. oceanicus*, the one host species in which it has been examined (Zuk *et al.*, 1993, 2006).

This study used field-based, two-speaker choice tests to examine the importance of *G. lineaticeps* calling song characters in host selection by female *O. ochracea*. Male *G. lineaticeps* produce a chirped calling song to attract females for mating, and conspecific females prefer calling songs with higher chirp rates and longer chirp durations (Wagner, 1996; Wagner *et al.*, 2001b; Wagner & Basolo, 2007). In some populations, singing males attract *O. ochracea*, and previous work – with a population different from the one studied here – suggested that the parasitoid flies, like female field crickets, preferentially orient to higher chirp rates and longer chirp durations (Wagner, 1996). Subsequent work, however, has shown that the stimulus values used in the previous study encompassed only a part of the natural range of variation in *G. lineaticeps* calling song for the population studied. In particular, the chirp rates used were below average, while the chirp durations used ranged from slightly below average to well above average. Thus, while it is clear the flies have preferences based on these two song characters, the forms of these preferences are not clear (i.e. whether the preferences are directional, stabilising, or disruptive over the range of natural variation). In addition, little is known about geographic variation in *Ormia* song preferences based on the song of a given host.

This study also examined the relative importance of male chirp rate and chirp duration in host selection by the flies. Two approaches were used, both of which involved pitting song characters against each other. First, the study tested whether the flies would prefer higher chirp rate/shorter chirp duration songs or lower chirp rate/longer chirp duration songs. Second, the study tested whether the flies would continue to prefer one song type to another when the previously non-preferred song type was presented at higher amplitude. Previous results have shown that the flies prefer higher to lower amplitudes (Wagner, 1996; Müller & Robert, 2002); increasing the amplitude of a particular song type should thus make it more attractive, and the extent to

which the amplitude of a non-preferred song type can be increased while still being discriminated against provides a measure of the strength of the preference (e.g. Gerhardt *et al.*, 2000). Very little is known about the relative importance of different song characters in host selection by phonotactic parasitoids, but this information is necessary for understanding how selection due to predation acts on host signalling behaviour.

## Methods

*Ormia ochracea* were studied at Rancho Sierra Vista in the Santa Monica Mountains National Recreation Area, located near Thousand Oaks, California. All preference tests were conducted between 30 July and 14 September 2004 in a 3-h period following sunset (the time period when the flies show the greatest phonotactic activity; Cade *et al.*, 1996).

To examine fly preferences, the following five synthetic calling songs were constructed that varied in chirp rate and/or chirp duration: (1) a low chirp rate and short chirp duration song (chirp rate = 1.8 chirps s<sup>-1</sup>, chirp duration = 90 ms); (2) a low chirp rate and long chirp duration song (chirp rate = 1.8 chirps s<sup>-1</sup>, chirp duration = 150 ms); (3) a high chirp rate and short chirp duration song (chirp rate = 4.2 chirps s<sup>-1</sup>, chirp duration = 90 ms); (4) a high chirp rate and long chirp duration song (chirp rate = 4.2 chirps s<sup>-1</sup>, chirp duration = 150 ms); and (5) an intermediate chirp rate and intermediate chirp duration song (chirp rate = 3.0 chirps s<sup>-1</sup>, chirp duration = 120 ms). The low chirp rates and short chirp durations are approximately 2SD below the population mean values for these traits, the high chirp rates and long chirp durations are approximately 2SD above the population mean values for these traits, and the intermediate chirp rates and intermediate chirp durations are near the population mean values for these traits (Wagner & Hoback, 1999; Wagner & Reiser, 2000; W.E. Wagner, unpublished). To construct each song, a single pulse was selected from a natural chirp (pulse duration = 11 ms, dominant frequency = 5.17 kHz). This pulse was then copied to produce three chirps that contained between 6 and 10 pulses, and thus chirps that varied in duration (inter-pulse interval was held constant at 4 ms). Song loops were then constructed that varied in chirp rate by varying the duration of the inter-chirp interval.

A two-speaker choice design was used to test fly preferences. Pairs of songs were broadcast from different channels of a Sony CD player (D-NS505) through Stith Recording amplified speakers (SME AFS-A70) that were placed 2 m apart in the field. Fly responses to eight pairs of songs were tested (Table 1; Fig. 1): (1) low chirp rate, short chirp duration vs. high chirp rate, short chirp duration; (2) low chirp rate, long chirp duration vs. high chirp rate, long chirp duration; (3) low chirp rate, short chirp duration vs. low chirp rate, long chirp duration; (4) high chirp rate, short chirp duration vs. high chirp rate, long chirp duration; (5) low chirp rate, short chirp duration vs. intermediate chirp rate, intermediate chirp duration; (6) intermediate chirp rate, intermediate chirp duration vs. high chirp rate, long chirp duration; (7) low chirp rate, long chirp duration vs. intermediate chirp rate, intermediate chirp duration; and (8) intermediate chirp rate, intermediate chirp duration vs. high chirp rate, short chirp duration.

**Table 1.** Responses of female *Ormia ochracea* to pairs of *Gryllus lineaticeps* calling songs that differed in chirp rate, chirp duration, and amplitude. 'Binomial *P*' presents the results of two-tailed binomial tests comparing the number of flies that responded to each of the paired song types. 'Change' presents the results of a Fisher's exact test comparing *O. ochracea* responses in each variable amplitude test to the equivalent equal amplitude test. Asterisks indicate significant changes in response compared with the equivalent equal amplitude test (after Bonferroni correction, critical  $\alpha=0.025$ ).

Stimulus pair	Chirp rate (chirps s <sup>-1</sup> )	Chirp duration (ms)	Chirp amplitude (dB SPL)	Number of flies attracted	Binomial <i>P</i>	Change
<i>Equal song amplitudes</i>						
1	1.8	90	93	1	<0.001	–
	4.2	90	93	19		
2	1.8	150	93	0	<0.001	–
	4.2	150	93	20		
3	1.8	90	93	2	<0.001	–
	1.8	150	93	18		
4	4.2	90	93	7	0.264	–
	4.2	150	93	13		
5	1.8	90	93	0	<0.001	–
	3.0	120	93	20		
6	3.0	120	93	1	<0.001	–
	4.2	150	93	19		
7	1.8	150	93	3	0.002	–
	3.0	120	93	17		
8	3.0	120	93	3	0.002	–
	4.2	90	93	17		
<i>Amplitudes of non-preferred song types increased by 50%</i>						
1	1.8	90	96	1	<0.001	1.000
	4.2	90	93	19		
2	1.8	150	96	2	<0.001	0.487
	4.2	150	93	18		
3	1.8	90	96	7	0.264	0.127
	1.8	150	93	13		
4	4.2	90	96	18	<0.001	<0.001*
	4.2	150	93	2		
5	1.8	90	96	2	<0.001	0.487
	3.0	120	93	18		
6	3.0	120	96	11	0.824	0.001*
	4.2	150	93	9		
7	1.8	150	96	5	0.042	0.695
	3.0	120	93	15		
8	3.0	120	96	14	0.116	0.001*
	4.2	90	93	6		
<i>Amplitudes of non-preferred song types increased by 100%</i>						
1	1.8	90	99	5	0.042	0.182
	4.2	90	93	15		
2	1.8	150	99	12	0.504	<0.001*
	4.2	150	93	8		
3	1.8	90	99	9	0.824	0.031
	1.8	150	93	11		
4	4.2	90	99	19	<0.001	<0.001*
	4.2	150	93	1		
5	1.8	90	99	6	0.116	0.020*
	3.0	120	93	14		
6	3.0	120	99	18	<0.001	<0.001*
	4.2	150	93	2		
7	1.8	150	99	15	0.042	<0.001*
	3.0	120	93	5		
8	3.0	120	99	17	0.002	<0.001*
	4.2	90	93	3		

Three sets of tests were conducted with each of the pairs of songs. In the first set, all songs were broadcast at 93 dB sound pressure level (SPL) (re: 20  $\mu$ Pa) measured at a distance of 30 cm from the speakers. In the second set, each song type preferred in the first set was broadcast at 93 dB SPL and the alternative non-preferred song type was broadcast at 96 dB SPL measured at a distance of 30 cm from the speakers (a 50% increase in amplitude). In the third set, each song type preferred in the first set was broadcast at 93 dB SPL and the alternative non-preferred song type was broadcast at 99 dB SPL measured at a distance of 30 cm from the speakers (a 100% increase in amplitude). Broadcast amplitudes were calibrated using a Brüel and Kjær 2236 sound level meter (fast RMS) prior to the start of each test.

Field broadcasts of the song pairs attracted nearby flies, and the number of flies that chose each of the alternative song types was recorded. A choice was scored when a fly either landed on a speaker or walked to the speaker and climbed upon the surface of the speaker. Each fly that responded was collected by covering it with a vial and then sliding stiff paper between the vial and the surface of the speaker. The vial was then lifted away from the speaker and the paper was replaced with a lid. The flies were then held to prevent resampling within a given test. If a test with a given pair of songs was completed the same night a fly was collected, it was released at the conclusion of the night's tests approximately 50 m from the testing location. If a test with a given pair of songs was not completed the same night a fly was collected, it was held until the end of the night on which the test was completed. As a result, each individual fly was only able to respond once in a given test, and only once in a given night, but might have responded in different tests that were conducted on different nights. After 10 flies responded in a given test, the stimuli were switched between the speakers to control for position effects, and after 20 flies responded in a given test, the test was halted. A total of 480 responses were recorded (20 responses per test  $\times$  24 tests). Whether the flies deposited larvae on the speakers was not assessed.

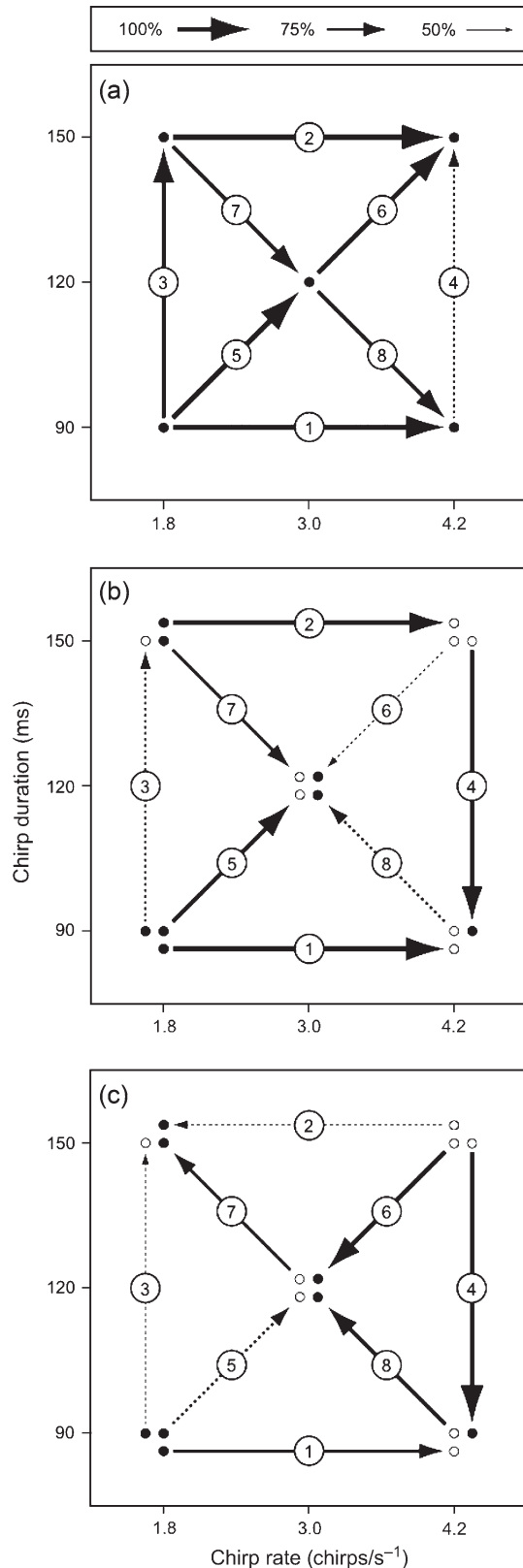
Fly responses to each of the two alternative song types was compared with a two-tailed binomial test. In addition, a Fisher's exact test was used to compare fly responses in each variable amplitude test to their responses in the equivalent equal amplitude test (the analyses were in the form of  $2 \times 2$  contingency tables) to determine if fly responses to a given pair of songs changed when the amplitude of the non-preferred song type was increased. Bonferroni corrections were used to control the family-wise error rate in these comparisons; because two comparisons were made among each set of three tests, the critical  $\alpha$  for each comparison was 0.025 ( $\alpha=0.05/2$ ).

## Results

### *Song types presented at equal amplitudes*

In the first set of tests, pairs of songs were broadcast that varied in chirp rate and/or chirp duration, but not in amplitude (Table 1, Fig. 1a). There were four primary results.

First, when chirp duration was held constant, the flies preferred higher chirp rates. Significantly more flies responded to the



high chirp rate song than to the low chirp rate song, regardless of whether the alternatives had short (pair 1) or long (pair 2) chirp durations.

Second, when chirp rate was held constant, the flies sometimes preferred longer chirp durations. Significantly more flies responded to the long chirp duration song than to the short chirp duration song when the alternatives had low chirp rates (pair 3). In contrast, there was not a significant difference in the number of flies that responded to the long and short chirp duration songs when the alternatives had high chirp rates (pair 4).

Third, when both chirp rate and chirp duration were varied and positively associated, the flies preferred higher chirp rate/longer chirp duration combinations. Significantly more flies responded to the high chirp rate/long chirp duration songs than responded to the low chirp rate/short chirp duration songs, regardless of whether the alternatives had below average and average trait values (pair 5) or average and above average trait values (pair 6).

Fourth, when both chirp rate and chirp duration were varied and negatively associated, the flies appeared to show stronger preferences for higher chirp rates than for longer chirp durations. Significantly more flies responded to the high chirp rate/short chirp duration songs than responded to the low chirp rate/long chirp duration songs, regardless of whether the chirp rates were below average and average (pair 7) or average and above average (pair 8).

#### Amplitudes of non-preferred song types increased by 50%

In the second set of tests, the amplitudes of the non-preferred song types in the first set of tests were increased by 50% relative to the alternatives (Table 1, Fig. 1b). There were five primary results.

First, when chirp duration was held constant, the flies preferred higher chirp rates even when the higher chirp rates were presented at lower amplitudes. Significantly more flies responded to the high chirp rate/low amplitude song than to the low chirp rate song/high amplitude song, regardless of whether the alternatives had short (pair 1) or long chirp (pair 2) chirp durations.

**Fig. 1.** Graphical representation of the responses of female *Ormia ochracea* to pairs of *Gryllus lineaticeps* calling songs that differed in chirp rate and/or chirp duration. (a) Each song type of a pair presented at equal amplitude (93 dB SPL). (b) The non-preferred song type within a pair presented at a 50% higher amplitude (96 dB SPL) than the preferred song type (93 dB SPL). (c) The non-preferred song type within a pair presented at a 100% higher amplitude (99 dB SPL) than the preferred song type (93 dB SPL). Lines with arrows connect each pair of songs tested. Arrows point to the song type within a pair that attracted the most flies. The widths of the lines and sizes of the arrows are proportional to the percentage of flies attracted to the more preferred song type. Solid lines indicate significant differences in fly responses to the two song types, and dotted lines indicate non-significant differences in fly responses to the two song types. The numbers in circles correspond to the test numbers in Table 1. In the unequal amplitude tests, closed circles indicate the song type within each pair of higher amplitude and open circles the song type within each pair of lower amplitude.

Second, when chirp rate was held constant, the flies did not prefer longer chirp durations when the longer chirp durations were presented at lower amplitudes. At the low end of the chirp rate range, there was not a significant difference in fly response to the long chirp duration/low amplitude song and short chirp duration/high amplitude song (pair 3). At the high end of the chirp rate range, significantly more flies responded to the short chirp duration/high amplitude song than to the long chirp duration/low amplitude song (pair 4).

Third, when both chirp rate and chirp duration were varied and positively associated, the flies sometimes preferred higher chirp rate/longer chirp duration/lower amplitude combinations. When the alternatives had below average and average trait values, significantly more flies responded to the high chirp rate/long chirp duration song presented at low amplitude than to the low chirp rate/short chirp duration songs presented at high amplitude (pair 5). In contrast, when the alternatives had average and above average trait values, there was not a significant difference in the number of flies that responded to the high chirp rate/long chirp duration song presented at low amplitude and to the low chirp rate/short chirp duration song presented at high amplitude (pair 6).

Fourth, when both chirp rate and chirp duration were varied and negatively associated, the flies sometimes preferred high chirp rate/short chirp duration/low amplitude combinations. When the alternatives had below average and average chirp rates, significantly more flies responded to the high chirp rate/short chirp duration songs presented at low amplitude than to the low chirp rate/long chirp duration songs presented at high amplitude (pair 7). In contrast, when the alternatives had chirp rates that were average and above average, there was not a significant difference in the number of flies that responded to the high chirp rate/short chirp duration songs presented at low amplitude and to the low chirp rate/long chirp duration songs presented at high amplitude (pair 8).

Fifth, there were three significant changes in the responses of the flies compared with their responses in the equal amplitude tests (Table 1). The lack of a preference for songs with longer chirp durations when chirp rate was held constant at the high end of the range changed to a preference for shorter chirp durations. The preference for songs with higher chirp rate/longer chirp duration combinations disappeared when the alternatives were average and above average, and the preference for songs with high chirp rate/short chirp duration combinations over songs with low chirp rate/long chirp duration combinations disappeared when the alternatives had chirp rates that were at the high end of the range and chirp durations that were at the low end of the range. None of the other responses showed a significant change.

#### *Amplitudes of non-preferred song types increased by 100%*

In the third set of tests, the amplitudes of the non-preferred song types in the first set of tests were increased by 100% relative to the alternatives (Table 1, Fig. 1c). There were five primary results.

First, when chirp duration was held constant, the flies sometimes preferred higher chirp rates presented at lower amplitudes.

At the low end of the chirp duration range, significantly more flies responded to the high chirp rate/low amplitude song than to the low chirp rate/high amplitude song (pair 1). At the high end of the chirp duration range, there was not a significant difference in fly response to the high chirp rate/low amplitude song and low chirp rate/high amplitude song (pair 2).

Second, when chirp rate was held constant, the flies did not prefer longer chirp durations when the longer chirp durations were presented at lower amplitudes. At the low end of the chirp rate range, there was not a significant difference in fly response to the long chirp duration/low amplitude song and short chirp duration/high amplitude song (pair 3). At the high end of the chirp rate range, significantly more flies responded to the short chirp duration/high amplitude song than to the long chirp duration/low amplitude song (pair 4).

Third, when both chirp rate and chirp duration were varied and positively associated, the flies did not prefer high higher chirp rate/longer chirp duration/lower amplitude combinations. When the alternatives had below average and average trait values, there was not a significant difference in the number of flies that responded to the high chirp rate/long chirp duration song presented at low amplitude and to the low chirp rate/short chirp duration song presented at high amplitude (pair 5). In contrast, when the alternatives had average and above average trait values, significantly more flies responded to the low chirp rate/short chirp duration song presented at high amplitude than to the high chirp rate/long chirp duration songs presented at low amplitude (pair 6).

Fourth, when both chirp rate and chirp duration were varied and negatively associated, the flies preferred low chirp rate/long chirp duration/high amplitude combinations. Significantly more flies responded to the low chirp rate/long chirp duration/high amplitude song than to the high chirp rate/short chirp duration/low amplitude song, regardless of whether the chirp rates were below average and average (pair 7) or average and above average (pair 8).

Fifth, there were significant changes in all but two of the responses of the flies compared with their responses in the equal amplitude tests (Table 1). The only responses that did not change were the preference for the high chirp rate song when chirp duration was held constant at the low end of the range, and the preference for long chirp duration song when chirp rate was held constant at the low end of the range. All other preferences either became significantly weaker or reversed direction.

## Discussion

When female *O. ochracea* in the field were presented *G. lineaticeps* calling songs that varied in chirp rate and/or chirp duration, but not in amplitude, they preferred to approach the songs with higher chirp rates, sometimes preferred to approach the songs with longer chirp durations, and preferred to approach the songs that simultaneously had higher chirp rates and longer chirp durations. These results agree with those of a previous study that examined the preferences of flies from a different population (Wagner, 1996), suggesting that preferences

for higher chirp rates and longer chirp durations may be common in populations of *Ormia* that attack *G. lineaticeps*. Because male *G. lineaticeps* with higher chirp rates and/or longer chirp durations will have a higher probability of attracting parasitoids, natural selection due to fly predation should tend to favour the evolution of lower chirp rates. Natural selection due to fly predation should also tend to favour the evolution of shorter chirp durations, although this may only be true for males that produce low chirp rates (Fig. 1a). It is not yet known whether fly predation has affected the evolution of male singing behaviour in *G. lineaticeps*, but studies of other systems have shown that fly predation can substantially reduce male lifetime reproductive success (Lehmann & Lehmann, 2006) and can affect the evolution of male song (Zuk *et al.*, 1993). In addition, female field crickets are potentially at risk of fly predation when they are in association with preferred males if they are near a male when a fly arrives or if viable larvae are present on the ground around a male (Cade, 1975; Adamo *et al.*, 1995b). Fly predation may thus also affect the evolution of female mating preferences, favouring weaker chirp rate and chirp duration preferences. How male singing behaviour and female mating preferences actually evolve, however, will depend on the relative magnitudes of the costs and benefits of producing preferred songs and of expressing mating preferences.

Wagner (1996) presented *O. ochracea* a choice between one high chirp rate/short chirp duration and one low chirp rate/long chirp duration song and found no difference in fly responses. While these previous results suggested that chirp rate and chirp duration might be equally important to the flies, three lines of evidence from the current study suggest that *O. ochracea* from the population studied here have stronger preferences based on chirp rate than based on chirp duration. This difference may reflect either spatial or temporal variation in fly preferences. First, the flies only showed a significant preference for longer chirps when they were associated with low chirp rates, whereas they showed significant preferences for higher chirp rates regardless of the associated chirp duration (Fig. 1a). Second, when the flies were presented songs of higher chirp rate/shorter chirp duration and lower chirp rate/longer chirp duration, they consistently preferred the higher chirp rate/shorter chirp duration songs (Fig. 1a). Third, an increase in the amplitudes of non-preferred song types had a larger effect on chirp duration preferences than on chirp rate preferences (Fig. 1b,c); whereas the flies continued to prefer some higher chirp rates even when the alternative low chirp rate song was presented at a 100% higher amplitude, they showed no preference for longer chirp durations when the alternative short chirp duration song was presented at only a 50% higher amplitude (and they even preferred some shorter chirp durations when they were presented at a higher amplitude). Because the flies expressed stronger preferences based on chirp rate than based on chirp duration, natural selection due to fly predation should result in stronger selection for lower chirp rates than for shorter chirp durations. Interestingly, female *G. lineaticeps* from at least some populations likewise have stronger preferences based on chirp rate than based on chirp duration (Wagner & Basolo, 2007); they appear to prefer conspecific males with higher chirp rates because these males provide products in their seminal fluid that increase female fecundity and fertility (Wagner *et al.*,

2001a; Wagner & Harper, 2003). Both natural selection due to fly predation and sexual selection due to female choice may thus be stronger on chirp rate than on chirp duration.

It is not clear why female *O. ochracea* prefer higher chirp rates and longer chirp durations. Müller and Robert (2001, 2002) found that chirp rate and duration had little effect on whether a fly could locate a singing male, and little effect on the speed of localisation. It thus seems unlikely that the flies prefer these song types because the males producing them are easier to localise. It is possible that male song is related to the male's quality as a host (Wagner, 1996), and that chirp rate is better correlated with host quality than is chirp duration, but this possibility has not been tested. It is also possible that the chirp rate and duration preferences reflect a more general ancestral preference for more energetic songs (longer and more rapidly repeated songs), rather than a response that evolved in the context of their interaction with *G. lineaticeps* (e.g. Ryan & Wagner, 1987; Basolo, 1990; Ryan, 1990). Many ormiines, for example, appear to prefer more energetic songs (Lehmann, 2003), suggesting the possibility of an ancestral bias in this group for more energetic song types. *Ormia ochracea*, however, prefers more energetic song types when attacking some species of field cricket (e.g. Wagner, 1996; Zuk *et al.*, 1998), but does not prefer more energetic song types when attacking other species of field cricket (e.g. Gray & Cade, 1999).

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## References

- Adamo, S.A., Robert, D. & Hoy, R.R. (1995a) Effects of a tachinid parasitoid, *Ormia ochracea*, on the behaviour and reproduction of its male and female field cricket hosts (*Gryllus* spp). *Journal of Insect Physiology*, **41**, 269–277.
- Adamo, S.A., Robert, D., Perez, J. & Hoy, R.R. (1995b) The response of an insect parasitoid, *Ormia ochracea* (Tachinidae), to the uncertainty of larval success during infestation. *Behavioral Ecology and Sociobiology*, **36**, 111–118.
- Basolo, A.L. (1990) Female preference predates the evolution of the sword in swordtail fish. *Science*, **250**, 808–810.
- Cade, W.H. (1975) Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science*, **190**, 1312–1313.
- Cade, W.H., Ciceran, M. & Murray, A.-M. (1996) Temporal patterns of parasitoid fly (*Ormia ochracea*) attraction to field cricket song (*Gryllus integer*). *Canadian Journal of Zoology*, **74**, 393–395.
- Endler, J.A. (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, **34**, 76–91.
- Endler, J.A. (1982) Convergent and divergent effects of natural selection on color patterns in two fish faunas. *Evolution*, **36**, 178–188.
- Gerhardt, H.C., Tanner, S.D., Corrigan, C.M. & Walton, H.C. (2000) Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). *Behavioral Ecology*, **11**, 663–669.

- Gray, D.A. & Cade, W.H. (1999) Sex, death and genetic variation: natural and sexual selection on cricket song. *Proceedings of the Royal Society of London B*, **266**, 707–709.
- Hedrick, A.V. & Kortet, R. (2006) Hiding behaviour in two cricket populations that differ in predation pressure. *Animal Behaviour*, **72**, 1111–1118.
- 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). *Zoologischer Anzeiger*, **242**, 107–120.
- Lehmann, G.U.C. & Lehmann, A.W. (2006) Potential lifetime reproductive success of male bushcrickets parasitized by a phonotactic fly. *Animal Behaviour*, **71**, 1103–1110.
- Lloyd, J.E. (1973) Firefly parasites and predators. *Coleopterists Bulletin*, **27**, 91–106.
- Mitchell, W.C. & Mau, R.F.L. (1971) Response of the female southern green stink bug and its parasite, *Trichopoda pennipes*, to male stink bug pheromone. *Journal of Economic Entomology*, **64**, 856–859.
- Müller, P. & Robert, D. (2001) A shot in the dark: the silent quest of a free-flying phonotactic fly. *Journal of Experimental Biology*, **204**, 1039–1052.
- Müller, P. & Robert, D. (2002) Death comes suddenly to the unprepared: singing crickets, call fragmentation, and parasitoid flies. *Behavioral Ecology*, **13**, 598–606.
- Noldus, L.P.J.J., van Lenteren, J.C. & Lewis, W.J. (1991) How *Trichogramma* parasitoids use moth sex pheromones as kairomones: orientation behaviour in a wind tunnel. *Physiological Entomology*, **16**, 313–327.
- Ryan, M.J. (1990) Sexual selection, sensory system, and sensory exploitation. *Oxford Surveys in Evolutionary Biology*, **7**, 157–195.
- Ryan, M.J., Tuttle, M.D. & Rand, A.S. (1982) Bat predation and sexual advertisement in a Neotropical anuran. *American Naturalist*, **119**, 136–139.
- Ryan, M.J. & Wagner, W.E. Jr. (1987) Mating asymmetries between species: female swordtails prefer to mate with heterospecifics. *Science*, **236** (595), 597.
- Tuttle, M.D. & Ryan, M.J. (1981) Bat predation and the evolution of frog vocalizations in the neotropics. *Science*, **214**, 677–678.
- Wagner, W.E. Jr. (1996) Convergent song preference between female field crickets and acoustically orienting parasitoid flies. *Behavioral Ecology*, **7**, 279–285.
- Wagner, W.E. Jr & Basolo, A.L. (2007) The relative importance of different direct benefits in the mate choices of a field cricket. *Evolution*, **61**, 617–622.
- Wagner, W.E. Jr & Harper, C.J. (2003) Female life span and fertility are increased by the ejaculates of preferred males. *Evolution*, **57**, 2054–66.
- Wagner, W.E. Jr & Hoback, W.W. (1999) Nutritional effects on male calling behaviour in the variable field cricket. *Animal Behaviour*, **57**, 89–95.
- Wagner, W.E. Jr, Kelley, R.J., Tucker, K.R. & Harper, C.J. (2001a) Females receive a life span benefit from male ejaculates in a field cricket. *Evolution*, **55**, 994–1001.
- Wagner, W.E. Jr & Reiser, M.G. (2000) The importance of calling song and courtship song in female mate choice in the variable field cricket. *Animal Behaviour*, **59**, 1219–1226.
- Wagner, W.E. Jr, Smeds, M.R. & Wiegmann, D.D. (2001b) Experience affects female response to male song in the variable field cricket *Gryllus lineaticeps* (Orthoptera, Gryllidae). *Ethology*, **107**, 769–776.
- Walker, T.J. (1986) Monitoring the flights of field crickets (*Gryllus* spp.) and a tachinid fly (*Euphasiapteryx ochracea*) in north Florida. *Florida Entomologist*, **69**, 678–685.
- Walker, T.J. & Wineriter, S.A. (1991) Hosts of a phonotactic parasitoid and levels of parasitism (Diptera: Tachinidae: *Ormia ochracea*). *Florida Entomologist*, **74**, 554–559.
- Zuk, M. & Kolluru, G.R. (1998) Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology*, **73**, 415–438.
- Zuk, M., Rotenberry, J.T. & Simmons, L.W. (1998) Calling songs of field crickets (*Teleogryllus oceanicus*) with and without phonotactic parasitoid infection. *Evolution*, **52**, 166–171.
- Zuk, M., Rotenberry, J.T. & Tinghitella, R.M. (2006) Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biology Letters*, **2**, 521–524.
- Zuk, M., Simmons, L.W. & Cupp, L. (1993) Song characteristics of parasitized and unparasitized populations of the field cricket *Teleogryllus oceanicus*. *Behavioral Ecology and Sociobiology*, **33**, 339–343.

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