Original article

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Bushcricket song structure and predation by the acoustically orienting parasitoid fly *Therobia leonidei* (Diptera: Tachinidae: Ormiini)

Abstract Males of most bushcricket species produce acoustic advertisement signals to attract females for mating. These signals can also increase conspicuousness to predators. In the genus *Poecilimon* (Orthoptera: Phaneropterinae) males are attacked by the parasitoid fly *Therobia leonidei* (Diptera: Tachinidae: Ormiini) which locates males by their calls. In Greece *T. leonidei* parasitizes several *Poecilimon* species with different song structures: we examined whether host choice is related to song structure by comparing parasitism rates in two closely related *Poecilimon* species. One of these species produces monosyllabic songs, the songs of the other species being polysyllabic. The tachinid fly parasitized the polysyllabic species to a greater extent. We demonstrate in a field-experiment that this preference for the polysyllabic species does not depend on local adaptations of the fly. The most probable explanation for the preference of the fly for the polysyllabic singing species seems to be better detection of longer songs. This result is discussed in the context of male song evolution.

Key words Acoustic communication · Host-parasitoid relationship · Ormiini · Tettigonoidea · Orthoptera

Introduction

In many animals, males possess traits that make them conspicuous to attract conspecific females for mating (Andersson 1994). Conspicuous acoustic signals are used to attract females by several species of birds, frogs, cicadas, and orthopterans. In one group of the Orthoptera, the bushcrickets (Tettigoniidae), male songs constitute secondary sexual characters (Darwin 1871) as they provide appropriate stimuli for attracting females (Bailey 1991). With sexual selection acting on song characters (summarized for gryllids in Gray 1997), the evolution of song could be expected to follow predictable patterns: continuously repeated song elements and the incorporation of complexity into the songs by varying the pulse rate and/or the intensity within trills or chirps are general features in gryllids (Otte 1992), Tettigonids (Heller 1990) and acridids (von Helversen 1986). Males with such repetitive or complex song patterns might be preferred by females for several reasons. In long-distance communication, such songs may be favored because they are easily localizable. Females would thereby minimize search time and reduce the risk of predation during approach (Grafe 1997).

However, the evolution of conspicuous signaling could be constrained by predation: enemies could exploit sexual signals to use the signaler as prey or host (Sakaluk 1990; Magnhagen 1991). Predators like bats (Belwood and Morris 1987), birds (Bell 1979) and two parasitoid fly families (reviewed by Burk 1982) use insect male calls to locate their prey. Prominent examples of acoustically orienting parasitoids of Orthoptera are tachinid fly species of the tribe Ormiini (Cade 1975; Lakes-Harlan and Heller 1992; Allen 1995). Besides others, the hosts of this Tachinidae include North American crickets. Studies on these field crickets, which produce trills of repetitive song elements continuously over minutes, have shown that interspecific variation in song structure can affect the attractiveness of songs to flies (Walker 1993). Males of cricket species that are parasitized by tachinid flies sing less than males of unparasitized species (Cade and Wyatt 1984). Within one gryllid species, male singing is reduced in populations parasitized by the tachinid fly *Ormia ochracea* in comparison with unparasitized populations (Cade 1981). Further, a number of differences in song characters between parasitized and unparasitized populations of the cricket *Teleogryllus oceanicus* (Zuk et al. 1993; Roten-

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berry et al. 1996) also seem to be a response to parasitism by *O. ochracea*. In gryllids, females prefer conspecific males whose songs are characterized by longer chirp duration and higher repetition rates. This is similar to the preference of female tachinid flies (Wagner 1995). For the ear of female *O. ochracea*, Robert et al. (1992) described a sharp tuning towards the best frequency of the song of *Gryllus rubens*. In addition, Walker (1993) demonstrated that *O. ochracea* shows selectivity for the song pattern of its main host *G. rubens*. It seems that male crickets are in a dilemma: conspecific female choice may drive the evolution of male songs to higher repetition rates and longer song duration, but selection by fly parasitism may result in generally reduced singing activity or reduced chirp duration in male crickets.

In contrast to *Ormia*, the European fly species, *Therobia leonidei* (Mesnil 1964) (Diptera: Tachinidae) is known to infect a variety of bushcricket species (Leonide 1969). All of the known bushcricket host species produce short chirps less than 1 s in length, repeated after pauses remarkably longer than the chirps themselves. Therefore they might be harder to detect than singing crickets. The broad tuning of the fly's ear (Stumpner and Lakes-Harlan 1996) reflects the broad frequency spectrum of the songs of its hosts (Leonide 1969), all of which have their peak song frequencies in the range of 12–28 kHz (Heller 1988). Among the known hosts of the fly are several species of the genus *Poecilimon* Fischer, 1854 (Tettigonioidea, Phaneropteridae) (Lakes-Harlan and Heller 1992; Lehmann 1998), which differ in singing behavior (Heller 1988). *Poecilimon* females and experimentally muted males were never infected (Lakes-Harlan and Heller 1992), showing that song production is necessary for parasitism.

We tested the hypothesis that songs with a longer duration lead to higher predation risk. We used two closely related species of the *Poecilimon propinquus* group that produce very distinct songs (Heller 1988) but are similar in other aspects such as activity patterns, body size, and population density (Heller 1984; Heller and von Helversen 1993). The main difference between *Poecilimon veluchianus* Ramme, 1933 and *Poecilimon mariannae* Willemse & Heller 1992 is the number of syllables per chirp, which ranges from 1 in *P. veluchianus* to 5–11 in *P. mariannae* (Heller 1988).

We predicted that the species with the polysyllabic song should be parasitized to a greater extent than the species with the monosyllabic song. The two species are parapatrically distributed (Willemse and Heller 1992). While *P. mariannae* is confined to the plains, *P. veluchianus* is found in the mountainous regions of central Greece.

For our study we (1) screened levels of parasitism of the two species in a number of populations over their range of distribution in Greece, and (2) tested the hypothesis experimentally in a two-way field experiment: to exclude the possibility that local parasitoid-host adaptations and ecological factors were responsible for different levels of parasitism in field populations, we introduced males of each species into a resident population of the other species.

Methods

Acoustic parameters

The sound pressure-level (dB SPL, maxpeak) was measured from a sample of nine males in each population. Ten recordings were made from each male. The SPL was measured dorsally at a distance of 10 cm from the males using a Brüel & Kjaer sound level meter (2231) in combination with a B&K 6.35-mm (= 1/4 in) condenser microphone (4135) and an external custom-made 2.6-kHz highpass filter.

Song recordings conducted for the frequency spectra analysis were made at a distance of 10 cm dorsally from the singing male using a B&K 6.35-mm microphone (4135), a B&K amplifier (2231), and a videorecorder modified to register sound (frequency response flat from 1 to above 60 kHz).

Frequency analysis by mean of a Fast Fourier Tranformation (power spectra of complete syllables) was performed on a MOSIP computer (program SPEKTRO 6.0, Fa. MEDAV) (Reinhold and Heller 1991).

The song structure of *P. mariannae* and *P. veluchianus* was first investigated by Heller [1984 (*mariannae* = *aegaeus*), 1988]. For this study, male songs of both populations were recorded in the field using an Uher tape recorder 4400 in combination with a condenser microphone (Uher 645 or Sennheiser ME66). With such recording equipment, only song components up to 20 kHz could be registered, but without altering the time-amplitude-structure of the recording. Measurements are given as means ± SD.

Body size

The length of the right hind femur of all investigated individuals was measured, a commonly used standard for body size in bushcrickets. Measurements are given as means ± SD.

Levels of parasitism in unmanipulated populations

To measure levels of parasitism for the two species in the field, five populations of both species – *P. mariannae* and *P. veluchianus* – were investigated in the years 1985–1996. Adult males were sampled randomly in each population. Parasitized males were counted as percent of all sampled individuals. Levels of parasitism were only sampled in mature populations–around 3 weeks after appearance of the first adult bushcrickets and without occurrence of any subadult individuals. In populations where more than one measurement was made in a season the maximal level of parasitism (in %) is given. We used χ^2 tests of independence for parasitism rates both between and within species. The α level of significance was corrected for multiple Fisher's exact-test comparisons between *P. veluchianus* populations using Bonferroni's formula [$p = \alpha/m$; m (number of multiple comparisons) $= n \times (n-1)/2$].

Visibility of parasitism

After locating a male bushcricket, the female fly deposits planidium larvae on the abdomen of the male, which burrow inside the host. A few days later, the larvae produce a connection with the air outside the host through a funnel in the host abdomen (Leonide 1969). Subsequently, the infection by the fly is indicated by a brown dot on the ventral side of the male's abdomen. To measure the delay between the larviposition and visible signs of parasitism, 125 unparasitized *P. mariannae* males were released for only one night (1–2 June 1996) near Vrissiá. At this time of the season, the attack

rate by the fly reaches its maximum. After recapture, the individuals were checked for the presence of parasites over the next 7 days.

Rate of parasitism during field experiments

During the field experiments in Greece, two species of *Poecilimon* were used: *P. veluchianus* Ramme, 1933 and *P. mariannae* Willemse & Heller 1992.

To exclude local effects as a possible explanation for differences in levels of parasitism between the two species, the field experiments were conducted in two parts: experiment I and II. In experiment I, males of *P. veluchianus* were introduced into a local population of *P. mariannae* near Vrissiá (central Greece, 22°19′E, 39°15′N). Experiment II took place in Kanália (central Greece, 21°59′E, 38°53′N) around 50 km away from Vrissiá. Males of *P. mariannae* were introduced into the local population of *P. veluchianus*. Since the fly attacks only adult hosts, *P. mariannae* and *P. veluchianus* males were collected as subadult individuals to ensure that they were not parasitized. After the final molt, each male was marked individually with reflective tape to aid in nocturnal relocation (Heller and von Helversen 1990). For the field experiments (I and II), an area of 50 m² was demarcated with wooden rods and surrounded with gauze up to a height of 80 cm as a protection against grazing sheep. This area was open from above, to ensure that the flies could approach easily.

At the beginning of the experiment, 50 marked *P. mariannae* males and 50 marked *P. veluchianus* males were placed inside the staked area. Every evening all males were recaptured from the field, checked for the presence of parasitoids and returned to the experimental area. To avoid effects of mating on calling activity and parasitism, females of the local species were removed. Males do not sing after copulation for the rest of the night and show reduced singing activity even on following nights (Heller and von Helversen 1993). The experiment was conducted for 20 days. Parasitized males were used for further experiments and not released back into the field.

To maintain a constant density of males, parasitized and missing individuals were replaced with other marked males, so that the number of 50 males was nearly constant for both species for the duration of the experiment. At the end of the experiment, all males were collected and observed for an additional 7 days to be sure that every infection was noticed. To control for variation in the number of days that males were exposed and then missed, "days of exposure in the field" were calculated. A male could have been exposed for a maximum of 20 days. Using 50 males per species per day the sum of "days of exposure in the field" could reach 1000 for each of the two species. For every male we counted the days in the enclosure minus time until the infection can normally be seen (4 days, see Results), e.g., for a male that could be found on 8 consecutive days after release (and was missed from the 9th day on), only 4 days of exposure were counted. But for an individual which was released for only 3 days and then missed, 0 days of exposure were counted because of the impossibility of detecting any parasitism. These individual days of exposure were summed for the two species *P. mariannae* and *P. veluchianus*. A χ^2 test of independence using a 2×2 table was made for the events of parasitism of the two species in relation to the days of exposure.

Parasitism rates in the experiment compared to the unmanipulated population in Kanália

In the field experiment, only parasitism rates per day were available, because parasitized males were removed daily from the enclosure. In contrast, samples collected on one day in the unmanipulated population contained parasitized males summed over the parasitizing events of a number of previous nights. Therefore the two sets were not equivalent. To compare the rates of parasitism inside and outside the enclosure, we converted the data found in our experiment by summing up the daily rates of para-

sitism and corrected these data for the natural mortality rate. We considered two types of mortality: (1) the daily mortality rate of males in the field (marked males recaptured on a given night divided by total number of marked males on the night before), and (2) mortality due to parasitism: freshly parasitized males placed in small cages and observed for mortality, the percent of surviving males being calculated every day (Lehmann and Heller 1997; Lehmann 1998). To find potential differences between the level of parasitism inside and outside the experimental area, the parasitism level for the population of *P. veluchianus* in Kanália was calculated for one night (12 June 1996).

Results

Acoustic parameters

The SPL of the song of *P. mariannae* (121 ± 2 dB, $n = 9$) is nearly the same as that of *P. veluchianus* (120 ± 2 dB, $n = 9$) (*t*-test, $df = 16$, $P = 0.33$).

Both species produce broad-band ultrasonic signals with a main component between 20 and 40 kHz. The spectra are very similar for both species with a peak frequency around 25 kHz (Fig. 1).

In the genus *Poecilimon*, only the closing movement of the wings produces a sound syllable. The two species examined have different song structures. In the polysyllabic species *P. mariannae,* the chirp consists of 5–11 repeated syllables (9 ± 1 syllables, $n = 12$ males) with a total song duration around 600 ms. The song is produced at a mean rate of 0.4 Hz. With a mean song duration of 600 ms, the interchirp-interval (ICI) lasts for 1.9 s. In *P. veluchianus*, the whole chirp includes only one such syllable (monosyllabic) which has a duration of about 80 ms ($n = 12$ males). The song is repeated at the same rate of 0.4 Hz (= every 2.5 s). The ICI, with a duration of 2.4 s is, on average, 0.5 s longer than in *P. mariannae* (Fig. 2). The duty cycle reaches 24% in *P. mariannae* and 3% in *P. veluchianus*.

Body size

The mean body size, measured as length of the right hind femur (*P. mariannae* 16.7 ± 0.7 mm, $n = 106$;
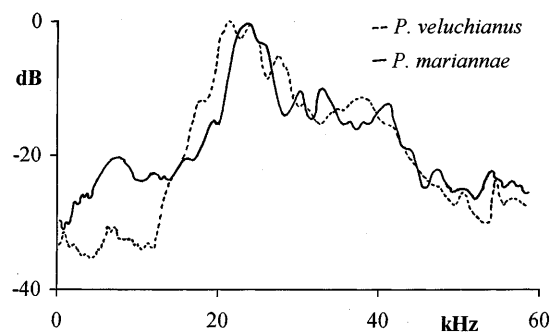

Fig. 1 Frequency spectra of *Poecilimon mariannae* and *P. veluchianus* (power spectra with units of decibels relative to maximum intensity)
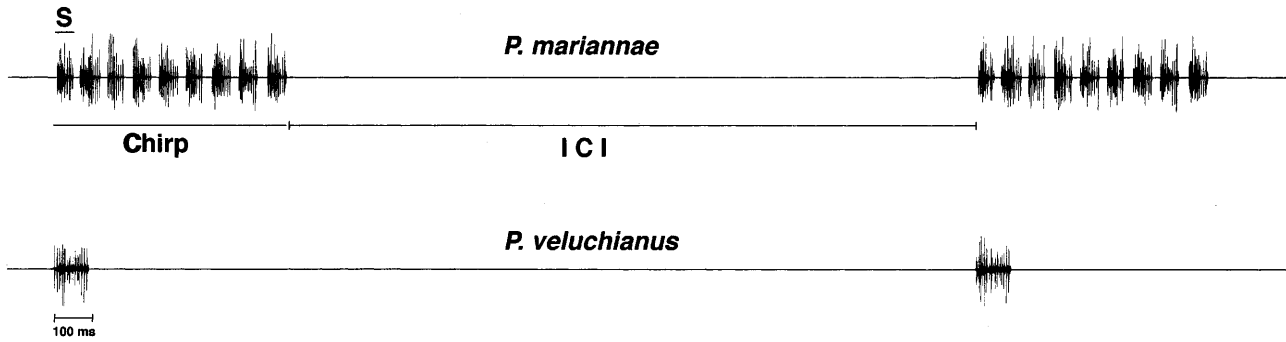
Fig. 2 Song structures of two consecutive chirps of *P. mariannae* and *P. veluchianus*. Marked are one chirp, one syllable (*S*) and the interchirp-interval (*ICI*). Recordings were made at a temperature of 24 °C

P. veluchianus 16.7 ± 0.6 mm, $n = 84$; *t*-test, $df = 188$, $P = 0.95$) was very similar for the males of the two species used in the field experiments.

Levels of parasitism in unmanipulated populations

Field populations of the polysyllabic species *P. mariannae* were typically parasitized to a greater extent than populations of the monosyllabic species *P. veluchianus* (Table 1). All sampled populations of *P. mariannae* were found to be infested. In contrast, a number of populations of the monosyllabic species *P. veluchianus* were not parasitized. In *P. veluchianus*, a population above Makirrahi (Nomos Fthiótida: 22°11′ E 38°52′ N) was found not to be parasitized in three consecutive years ($n = 150, 200, 180$). Because we cannot be sure that *T. leonidei* inhabits this region, the data are not included in Table 1. For statistical comparison we used χ^2 tests for independence separately for both species. While the seven samples of *P. mariannae* did not significantly differ in their levels of parasitism ($\chi^2 = 8.88$, $df = 6$, $P = 0.18$), the samples of *P. veluchianus* did show significant difference ($\chi^2 = 39.74$, $df = 1$, $P < 0.001$). A pairwise comparison between the samples of *P. veluchianus* showed significant differences between the population of Ellinópirgos and three of the remaining six samples due to the low number of parasitized males found in this population (Fisher's exact test, $df = 1$, $P < 0.00048$, corrected for multiple comparison, $p = \alpha/m = 21$). In addition, the population in Kanália in 1996 had the highest level of parasitized *P. veluchianus* males, differing significantly from the level in 1995 and the level in the Mesochóri population (Fisher's exact test, $df = 1$, $P < 0.0024$). Neglecting the differences within the species *P. veluchianus* and using the mean of all seven samples for each of the two species, a comparison between *P. veluchianus* and *P. mariannae* revealed a highly significant difference in parasitism rate ($\chi^2 = 13.9$, $df = 1$, $P < 0.001$). On average, there was a threefold higher level of parasitism in *P. mariannae* (51%) than in *P. veluchianus* (14%).

Visibility of parasitism

A total of 117 individuals of the 125 *P. mariannae* that were set free for one night were recaptured at the end of the night. Within the next 7 days, 15 males had been parasitized. The spot on the abdomen signifying the presence of the larva typically appears 4–5 days after infection; 80% of parasitism can be seen 4 days after infection (Fig. 3).

Table 1 Levels of parasitism by the fly *Therobia leonidei* in unmanipulated populations of the two closely related bushcricket species *Poecilimon mariannae* and *P. veluchianus*

Locality	Nomos	Coordinates	Species	Parasitized males max. % [n (100%)]	Year
Loutró	Lárissa	22°13′E 39°33′N	*mariannae*	20.0 ($n = 10$)	1995
Mouzáki	Karditsa	21°40′E 39°26′N	*mariannae*	42.2 ($n = 64$)	1992
Vrissiá	Lárissa	22°19′E 39°15′N	*mariannae*	57.4 ($n = 54$)	1994
	Lárissa	22°19′E 39°15′N	*mariannae*	50.0 ($n = 36$)	1995
	Lárissa	22°19′E 39°15′N	*mariannae*	53.7 ($n = 54$)	1996
Vardali	Fthiótida	22°19′E 39°12′N	*mariannae*	62.5 ($n = 8$)	1995
Perivóli	Fthiótida	22°11′E 39°04′N	*mariannae*	65.0 ($n = 20$)	1995
Ellinópirgos	Karditsa	21°44′E 39°24′N	*veluchianus*	1.3 ($n = 80$)	1995
Mount Spilia	Árta	21°12′E 39°22′N	*veluchianus*	21.7 ($n = 23$)	1995
Palaeovráha	Fthiótida	22°03′E 38°54′N	*veluchianus*	24.1 ($n = 58$)	1996
Kanália	Fthiótida	21°59′E 38°53′N	*veluchianus*	10.3 ($n = 39$)	1994
	Fthiótida	21°59′E 38°53′N	*veluchianus*	8.9 ($n = 79$)	1995
	Fthiótida	21°59′E 38°53′N	*veluchianus*	36.0 ($n = 50$)	1996
Mesochóri	Fthiótida	22°11′E 38°52′N	*veluchianus*	8.9 ($n = 45$)	1985

Fig. 3 Appearance of the breathing funnel produced by the fly larvae after parasitism

Fig. 5 Comparison of the rates of parasitism in *P. mariannae* (polysyllabic) and *P. veluchianus* (monosyllabic) as males parasitized per day (%) in experiment *I* and experiment *II* (***$P < 0.001$). The *arrow* indicates the local species. The *numbers* show parasitized males and days of exposure (different numbers result from differences in mortality due to predation)

Rate of parasitism during field experiments

The number of parasitized males increased continuously over the exposure period in both experiments. The 5 days without any event of visible parasitism at the beginning of both experiments can be explained by the delay until the breathing funnel of the larvae can be seen (see Fig. 3). The increase is nearly linear for both experiments and there were no site-specific differences (Fig. 4).

Seventy-nine percent of the parasitized males in Vrissiá and 70% in Kanália belonged to the species *P. mariannae*. Taking the different mortality rates for the two species in the field into account by calculating the days of exposure, this gave a ratio of infected males of *P. mariannae* to *P. veluchianus* of 3.8 and 3.3 in the two experiments. The result was the same for both experiments: males of *P. mariannae* (polysyllabic) were parasitized to a greater extent than *P. veluchianus* (monosyllabic), no matter which was the local 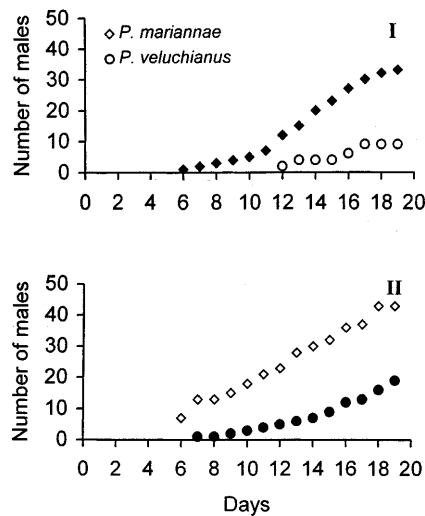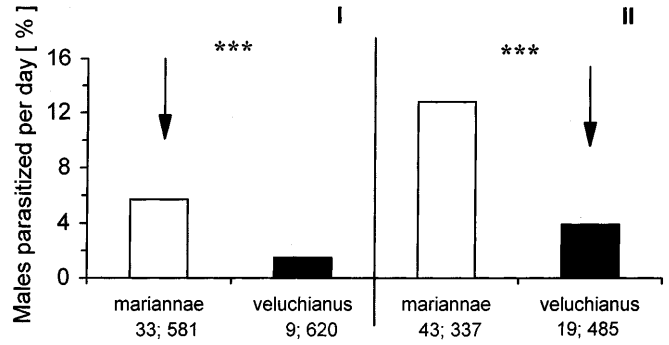resident species (Fig. 5). A test of independence using a 2×2 table gave a highly significant result for both experiment I ($\chi^2 = 14.80$, $df = 1$, $P < 0.001$) and experiment II ($\chi^2 = 18.92$, $df = 1$, $P < 0.001$).

Parasitism rates in the experiment compared to the unmanipulated population in Kanália

The rate of parasitism for *P. veluchianus* in Kanália ranges from 2.1 to 7.7%, with a mean of 3.7% per night. The daily survival rate for *P. veluchianus* males was 92.6%. Using these data, the total proportion of parasitized males inside the enclosure of the field experiment could be calculated as 31.7% on 12. June 1996. A sample of 50 males checked for parasitism in the unmanipulated population 100 m away from the staked area showed an equal level of parasitism at 32%.

Fig. 4 Cumulative number of parasitized males in experiments *I* and *II* over the period of 20 days. In both graphs the local species is marked by *solid symbols*, the introduced species by *open symbols*

Discussion

Results of the experiments described above showed that the choice of a bushcricket host by the phonotactic tachinid fly *T. leonidei* was related to song structure. The fly parasitized the polysyllabic species *P. mariannae* to a greater extent than the monosyllabic *P. veluchianus*. Female flies parasitized more than three times (3.8/3.3) as many *P. mariannae* males as *P. veluchianus* males. This preference for the species with polysyllabic songs was independent of whether it was the local resident or the introduced species. Therefore, local adaptations of the fly to its natural host species or to ecological factors are an unlikely explanation for the constancy of this preference in both experiments. All additional factors (SPL, frequency of song, body size) that were measured showed no differences between the two species. Although it is possible that other unknown factors are involved in the preference for *P. mariannae* as a host, song structure is the most likely explanation for this preference of the fly.

Several adaptations of crickets have been interpreted as mechanisms to avoid parasitism by ormiine flies (Cade 1981; Cade and Wyatt 1984; Zuk et al. 1993). Ormiine flies are active from sunset to sunrise (Cade et al. 1996) and parasitize only nocturnal-calling species. Both investigated species are active at night (Heller and von Helversen 1993). For *T. leonidei*, no direct evidence for nocturnal activity has yet been shown, but day-active species like *P. jonicus* were never found to be parasitized (personal observations). Thus the preference of the fly for males of the polysyllabic species *P. mariannae* is best seen as a direct response to song structure.

Direct measurement of the fly preferences with playback experiments could provide an even clearer result, but in *T. leonidei* this is a very difficult task: the attack rate of the flies on their hosts ranges from only 2 to a maximum of 13% per night (see Fig. 5). No flies could be attracted with simple traps (see Fowler 1988), traps with singing males or loudspeakers (personal observations). This is in contrast to some North American species of the genus *Ormia*, which could be attracted to loudspeakers quite easily and in high numbers (Cade 1975: Fowler 1988; Walker 1993).

The preference of the fly for species with the longer-lasting polysyllabic song structure agrees well with results on related fly species. Higher chirp rates and longer chirp duration were preferred by *O. ochracea*, even when these songs were of lower amplitude (Wagner 1995).

The duty cycle also plays an important role in determining the attractiveness of gryllid songs to *O. ochracea*. Walker (1993) found that artificial songs with duty cycles between 20 and 80% attracted flies, but songs with a duty cycle of less than 20% were ignored. *Therobia* accept a species with much lower duty cycles (3% in *P. veluchianus*), but prefer the species with the higher one (24% in *P. mariannae*). Despite the similarities, differences exist in the host range. For *O. ochracea*, only few host species were known and the song pattern of one special host (*G. rubens*) was significantly preferred over other tested songs from related *Gryllus* species, which were completely ignored or attracted only very few flies (Walker 1993). In *T. leonidei*, females have no main host, but parasitize several species over a range of different bushcricket families (Leonide 1969; Lakes-Harlan and Heller 1992; Lehmann 1998).

A plausible explanation for the higher levels of parasitism in *P. mariannae* males than in *P. veluchianus* males could be that the song of *P. mariannae* might be easier to localize than the song of *P. veluchianus* due to the higher duty cycle. There are additional hints which support this hypothesis of localization: Both species were parasitized in experiment I although *P. mariannae* males were dominant in the population outside the marked area. If the flies had a strong preference for *P. mariannae* males they could have avoided males of the other species completely. In experiment II, where *P. veluchianus* was the resident species and *P. mariannae* was introduced, the level of parasitism in the experiment could be calculated as 31.7% for *P. veluchianus* and 65.9% for *P. mariannae* on 12. June 1996. Outside the experimental area, the level of parasitism for the population of *P. veluchianus* was also 32%. It seems that the flies were not able to attack more individuals of *P. veluchianus* at this given population density. This idea was also supported by the result that the mean levels of parasitism for populations with *P. mariannae* was 51%, but only 14% for *P. veluchianus* (see Table 1). Increasing syllable number may increase the possibility of detection by the fly. Therefore, the number of syllables per chirp may reflect the balance between female preference and parasitoid pressure (Darwin 1871; Sakaluk 1990; Endler 1992). Despite the lack of direct evidence, better song detection should reduce time spent in host finding, which is consistent with foraging theory, summarized for parasitoids by Godfray (1994).

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