

Male Bushcrickets Favoured by Parasitoid Flies when Acoustically more Attractive for Conspecific Females (Orthoptera: Phanopteridae / Diptera: Tachinidae)

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LEHMANN G U C, HELLER K-G & LEHMANN A W [Dep Zool II, Univ, D-91058 Erlangen]: **Male Bushcrickets Favoured by Parasitoid Flies when Acoustically more Attractive for Conspecific Females (Orthoptera: Phanopteridae / Diptera: Tachinidae).**- Entomol Gener 25(2): 135-140; Stuttgart 2001-03. --- [Article]

In many animals, males [MM] have traits that increase their attractiveness to females [FF]. Their signals, however, can also increase conspicuousness to predators. In the bushcricket *Poecilimon thessalicus* Brunner von Wattenwyl 1891, MM are attacked by the parasitoid ormiine fly *Therobia leonidei* (Mesnil 1965) that locate them through their calls. MM, parasitized by the fly in a field experiment, attracted more conspecific FF in a previous phonotactic experiment than unparasitized MM. This result suggests that calling behaviour, which increases a M's probability of attracting a F, also increases his risk of attracting parasitoids. This supports the idea that sexual selection favours male adaptations that lead to high reproductive success even at the cost of increased predation.

Key words: *Poecilimon thessalicus* Brunner von Wattenwyl 1891 - *Therobia leonidei* (Mesnil 1965) - Acoustic communication - female choice - host-parasitoid relationship - sexual selection

LEHMANN G U C, HELLER K-G & LEHMANN A W [Dep Zool II, Univ, D-91058 Erlangen]: **Bevorzugung von Laubheuschrecken-Männchen durch parasitoide Raupenfliegen bei höherer akustischer Anziehungskraft für arteigene Weibchen (Orthoptera: Phanopteridae / Diptera: Tachinidae).**- Entomol Gener 25(2): 135-140; Stuttgart 2001-03.- [Abhandlung]

Bei vielen Tierarten besitzen die Männchen [MM] Eigenheiten, welche ihre Attraktivität für Weibchen [FF] erhöhen. Diese Signale können aber auch die Auffälligkeit gegenüber Prädatoren verstärken. Bei der Laubheuschrecken-Art *Poecilimon thessalicus* Brunner von Wattenwyl 1891 werden die MM von der parasitoiden Raupenfliege *Therobia leonidei* (Mesnil 1965) anhand ihrer Gesänge lokalisiert. MM, die in einem Freilandexperiment von der Fliege parasitiert worden waren, lockten in einem vorangegangenen Phonotaxis-Experiment mehr FF an als unparasitierte MM. Dieses Ergebnis suggeriert, daß ein Gesangsverhalten, das die Wahrscheinlichkeit eines M erhöht, ein F anzulocken, auch sein Risiko verstärkt, von Parasitoiden befallen zu werden. Damit wird die Idee unterstützt, daß sexuelle Selektion Männchen-Anpassungen fördert, welche zu einem erhöhten reproduktiven Erfolg führen, auch unter den Kosten einer verstärkten Prädation.

Schlüsselbegriffe: *Poecilimon thessalicus* Brunner von Wattenwyl 1891 - *Therobia leonidei* (Mesnil 1965) - Akustische Kommunikation - Phonotaxis - Sexuelle Selektion - Weibchenwahl - Wirt-Parasitoiden-Wechselwirkung

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1 Introduction

Males [MM] of many species have traits that increase their attractiveness to females [FF]. These traits, consisting of displays involving visual, olfactory and acoustic signals, are thus subject to sexual selection [ANDERSSON 1994]. Such signals may increase the animals' conspicuousness to predators [MAGNHAGEN 1991] or prey [GREY & GREY 1996] and, therefore, have to be considered as costs of mating [GWYNNE 1989]. The evolution of sexually selected traits may be opposed by natural selection, as first suggested by DARWIN [1871] and demonstrated by ENDLER [1992].

A group of animals which typically communicate by sound are the Orthoptera: Ensifera which include crickets and bushcrickets. The main function of song characters is to attract conspecific FF for mating [BAILEY 1991]. Males of certain Ensifera species are known to be preferred by conspecific FF [HEDRICK 1986, GRAY 1997] and are therefore likely to be influenced by sexual selection. Neotropical bats [BELWOOD & MORRIS 1987] and parasitoid flies of the tachinid tribe Ormiini [LEONIDE 1969, LEHMANN 1998, ZUK & KOLLORU 1998] are acoustically orienting natural enemies of singing Orthoptera. The latter possess an unique hearing organ which enables them to locate their hosts acoustically [LAKES-HARLAN & HELLER 1992, ROBERT et al 1992, 1994]. The degree of parasitism by ormiine flies can be very high with up to 60 percent of the MM in populations of the bushcricket *Poecilimon mariannae* Willemsse & Heller, 1992 being parasitized in three consecutive years [LAKES-HARLAN & HELLER 1992, LEHMANN & HELLER 1998]. Selected bushcricket species in North America [BURK 1982] and Australia [ALLEN 1995b] also show high levels of parasitism over periods of months.

Populations of North American Gryllidae that are under high pressure of Ormiini attack, show a number of reductions in song characters, in order to reduce the level of parasitism by the parasitoids [CADE 1981, CADE & WYATT 1984, ZUK et al 1993]. In California, WAGNER [1995] demonstrated that FF of *Gryllus lineaticeps* and its parasitoid fly *Ormia ochracea* Bigot 1873 both prefer the same song types of the male calling song. In contrast to the North American species, the only European Ormiini fly *Therobia leonidei* (Mesnil 1965) has a remarkably broad range of tettigoniid hosts within three families (Ephippigeridae, Tettigoniidae, Phaneropteridae) [LEONIDE 1969, LAKES-HARLAN & HELLER 1992, LEHMANN 1998].

All recorded hosts produce short chirps less than one second in duration, that are repeated after intervals remarkably longer than the chirp themselves. A comparison of other host species in the *Poecilimon propinquus*-group, which differ in their calling song patterns, showed a significant preference by the fly for the species with longer verses, that contain more syllables in the song [LEHMANN & HELLER 1998].

The monosyllabic species *P. thessalicus* was chosen to test whether MM that are attractive to conspecific FF suffer from more parasitism by *T. leonidei* in the field.

2 Methods

Poecilimon thessalicus is a flightless bushcricket (approximately 2 cm long) found on shrubs and bushes, the MM of which produce a mono-syllabic call at night to attract FF. FF do not answer MM songs but approach them silently. The study consisted of two experiments, one phonotactic experiment under semi-laboratory conditions and one field experiment with the previously tested individuals. Both experiments were performed in July 1996 near Elatohori (Central Greece, Pieria-Mountains, 22°16' E / 40°19' N) where the local *P. thessalicus* population had shown high levels of parasitism by the phonotactic fly *T. leonidei* in previous years [LEHMANN 1998].

Since the fly attacks only adult calling MM, *P thessalicus* MM were collected as nymphs in order to ensure that they were not parasitized. After their final moult 120 randomly chosen MM were marked individually with reflective tape and a number [HELLER & HELVERSEN 1990]. The acoustic attractiveness of MM to conspecific FF was tested in a phonotactic experiment.

All MM used were approximately two weeks after their final adult moult in age. The FF used were also collected as nymphs, aged for approximately 10 days after their final adult moult with 20 selected randomly from a pool containing 100 virgin individuals. For each phonotactic experiment four MM were put individually into four gauze cages (10 x 10 x 10 cm). After the MM began to sing, all four cages were placed on the upper side of a cage (length 1.20m x width 0.80m x height 0.60m) containing the 20 virgin FF initially position in the centre of base of the cage. MM sang continuously throughout the duration of the trials, and no synchronisation was apparent between their songs. The distances to each cage containing a singing M were approximately the same for all FF. As a measure for female response, the number of FF was taken that were within a distance of 10 cm to each M cage after 10 min. The chosen distance of 10 cm equals to when the two sexes are in antennae contact and the M stops singing.

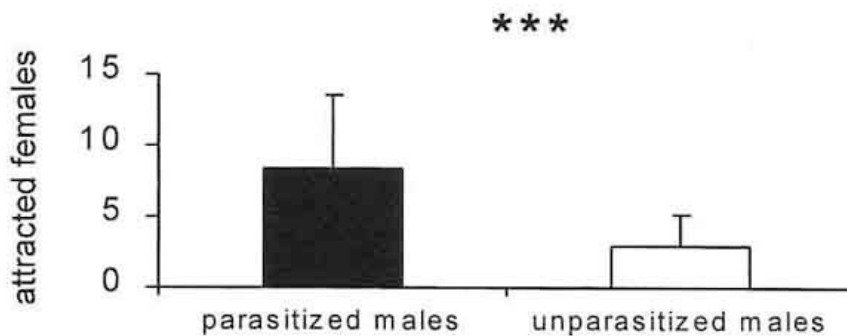


Fig 1: Number of attracted females (mean ± SD) by males found parasitized (black, n = 13) or unparasitized (white, n=49).

In the experiment, MM and FF had no physical contact with each other, so MM continued to sing. Typically FF either approached very close to singing MM or did not respond at all. After each trial the FF were replaced on the bottom of the cage. To avoid effects of position, the four boxes, containing the MM were interchanged randomly without disturbing the singing MM and the experiment was repeated. This procedure was done four times using the same MM and FF, so that every MM was tested in every position. The number of FF attracted within the four trials was added and the mean noted for each of the four MM to avoid the phenomenon of pseudoreplication [MACHLIS et al 1985]. The attractiveness of the MM was measured in this way because it was impossible to test every MM against the 119 other ones.

The phonotactic experiments were performed over four nights. In order to account for any effects of body-size, the length of the right hindfemur of all MM was measured.

For the field experiment, an area of 50 m², open from above, was demarcated with wooden rods and surrounded with gauze 80 cm high. The 120 individually marked and identified *P thessalicus* MM from the previous phonotactic experiment were placed inside the staked area. FF of the local population within the enclosure were removed, so MM could not mate.

The experiment was run for 5 days. After 5 days, all the remaining MM were collected and checked for the presence of parasitoid fly larvae. The presence of a fly larva can be recognised by a brown hole on the ventral side of the bushcricket abdomen [ALLEN 1995a]. This indicates the breathing funnel within, which is produced by the fly larva about 4 days after infection in *P thessalicus* [LEHMANN & HELLER 1998]. All individuals were observed for 7 additional days to be sure that every infection was noticed.

The average across parasitized MM of the mean number of FF showing positive phonotaxis to each MM was compared to the average number of FF showing positive phonotaxis to unparasitized MM. The presence or absence of significant differences in levels of parasitism between the two groups of MM was evaluated using a t-test.

3 Results

Of the 120 MM released in the field experiment, 62 were recaptured after five days. Out of these, 13 MM were parasitized, each by one larva of the acoustically orienting fly *T leonidei*. The parasitized MM attracted significantly more conspecific FF (Fig. 1) in the phonotactic choice experiment (mean \pm SD: 8.4 ± 5.1 , $n = 13$) than the unparasitized MM (3.0 ± 2.2 , $n = 49$) (T-test_{heterogen Variances}: $t = -3.75$, $FG = 13.24$, $P < 0.001$). The body length (mean \pm SD) for parasitized 14.89 ± 0.60 mm ($n = 13$) and for unparasitized MM 14.85 ± 0.52 mm ($n = 49$) was not significantly different (T-test, $f = 1$, $p = 0.93$).

4 Discussion

In *Poecilimon thessalicus*, the results show that MM preferred by conspecific FF also have a higher risk of being parasitized by *T leonidei* after release into the field. This supports the idea that sexual selection favours MM adaptations that lead to high reproductive success, even at the cost of increased predation or parasitism [BURK 1982].

However, just why are sexually more attractive MM also more attractive to flies? For one, it is unknown whether FF bushcrickets and parasitoid flies use the same sensory parameters to locate MM. Although it is clear that female bushcrickets use conspecific song (acoustic cues) to recognise and orient towards a prospective mate, it is possible that female *T leonidei* may locate MM using non-acoustic cues. In related Ormiini fly species, the song of the host alone is sufficient for host detection [CADE 1975]. There is also strong evidence that FF of *T leonidei* locate their hosts using mainly acoustic cues: the specialised ears of *T leonidei* show a tuning to the carrier frequency of the song of their hosts and FF and mute MM are never parasitized [LAKES-HARLAN & HELLER 1992]. A species of *Poecilimon* with poly-syllabic songs suffers a higher risk of being parasitized by *T leonidei* than a species with a monosyllabic song [LEHMANN & HELLER 1998]. The most probable explanation why some MM are parasitized is the better detectability and/or locatability by female flies. WAGNER [1995] found similar preferences by FF crickets and a parasitoid fly for songs containing higher repetition rates and longer chirp duration.

Search costs are frequently cited as a factor influencing mate and host preference [SEARCY & ANDERSSON 1986, GODFRAY 1994]. In *P veluchianus* Ramme 1933, another member of the *propinquus*-group, the survival of adult FF is lower than that in *P affinis* and is attributed to predation by hunters like spiders during mate searching by FF of *P veluchianus* [HELLER 1992]. Thus, in *P veluchianus* with high search costs FF may have evolved to prefer the MM that can be reached in the shortest possible time.

For *T. leonidei* the time spent searching for hosts must also be taken into account, as predicted by foraging theory [STEPHENS & KREBS 1986]. Thus MM producing more easily locatable songs would reduce the search costs for both bushcrickets and flies. In tests with crickets, regular and longer lasting synthetic calls seemed to be easier for the *Ormia ochracea* fly to detect [WALKER 1993]. Sound intensity may also have the same effect [WAGNER 1995]. It seems to be a general trend that selection favours MM producing the loudest/longest calls, minimising the costs of locating conspecific MM for FF. This type of selection for more elaborate calls could be expected according to the sensory exploitation hypothesis [RYAN & KEDDY-HECTOR 1992].

5 References

- ALLEN G R [1995a]: The calling behaviour and spatial distribution of male bushcrickets (*Sciarasaga quadrata*) and their relationship to parasitism by acoustically orienting tachinid flies.- *Ecol Entomol* **20**: 303-310; London / Great Britain.
- ALLEN G R [1995b]: The biology of the phonotactic parasitoid, *Homotrixa* sp. (Diptera: Tachinidae), and its impact on the survival of male *Sciarasaga quadrata* (Orthoptera: Tettigoniidae) in the field.- *Ecol entomol* **20**: 103-110; London / Great Britain.
- ANDERSSON M [1994]: *Sexual Selection*.- Princeton University Press; Princeton / USA.
- BAILEY W J [1991]: *Acoustic behaviour of insects. An Evolutionary Perspective*.- Chapman and Hall, London / Great Britain.
- BELWOOD J J & MORRIS G K [1987]: Bat predation and its influence on calling behavior in neotropical katydids.- *Science* **238**: 64-67; Washington / USA.
- BURK T [1982]: Evolutionary significance of predation on sexually signalling males.- *Fla entomol* **65**: 90-104; Gainesville / USA.
- CADE W H [1975]: Acoustically orienting parasitoids: fly phonotaxis to cricket song.- *Science* **190**: 1312-1313; Washington / USA.
- CADE W H [1981]: Alternative mate strategies: genetic differences in crickets.- *Science* **212**: 563-564; Washington / USA.
- CADE W H & WYATT D R [1984]: Factors affecting calling behaviour in field crickets, *Teleogryllus* and *Gryllus* (age, weight, density, and parasites).- *Behaviour* **88**: 61-75; Leiden / Nederland.
- DARWIN C [1871]: *The descent of man, and selection in relation to sex*.- Murray; London / Great Britain.
- ENDLER J A [1992]: Signals, signal conditions, and the direction of evolution.- *Am Nat* **139**: S125-S153; Chicago / USA.
- GODFRAY H C J [1994]: *Parasitoids: behavioral and evolutionary ecology*.- Princeton University Press; Princeton / USA.
- GRAY D A [1997]: Female house crickets, *Acheta domesticus*, prefer the chirps of large males.- *Anim Behav* **54**: 1553-1562; London / Great Britain.
- GREYER G F & GREY R M [1996]: Novel cost of a sexually selected trait in the rubyspot damselfly *Hetaerina americana*: conspicuousness to prey.- *Behav Ecol* **7**: 465-473; Oxford / USA.
- GWYNNE D T [1989]: Does copulation increase the risk of predation? - *Trends Ecol Evol* **4**: 54-56; Amsterdam / Nederland.
- HEDRICK A V [1986]: Female preferences for male calling bout duration in a field cricket.- *Behav Ecol Sociobiol* **19**: 73-77; Heidelberg / Bundesrepublik Deutschland..
- HELLER K-G [1992]: Risk shift between males and females in pair forming behavior of bushcrickets.- *Naturwissenschaften* **79**: 89-91; Berlin / Bundesrepublik Deutschland..

- HELLER K-G & HELVERSEN O von [1990]: Survival of a phaneropterid bush-cricket studied by a new marking technique (Orthoptera: Phaneropteridae).- *Entomol Gener* **15**: 203-208; Stuttgart / Bundesrepublik Deutschland..
- LAKES-HARLAN R & HELLER K-G [1992]: Ultrasound-sensitive ears in a parasitoid fly.- *Naturwissenschaften* **79**: 224-226; Berlin / Bundesrepublik Deutschland..
- LEHMANN G [1998]: Der Einfluß der phonotaktischen parasitoiden Fliege *Therobia leonidei* (Tachinidae, Ormiini) auf die akustische Kommunikation von Laubheuschrecken (Tettigonioidea, Phaneropteridae).- Ph.D. thesis; University Erlangen-Nürnberg / Bundesrepublik Deutschland..
- LEHMANN G U C & HELLER K-G [1998]: Bushcricket song structure and predation by the acoustically-orienting parasitoid fly *Therobia leonidei* (Diptera: Tachinidae: Ormiini).- *Behav Ecol Sociobiol* **43**:239-245; Heidelberg / Bundesrepublik Deutschland..
- LEONIDE J-C [1969]: Les ormiini- étude de *Plesiocestrus leonidei* Mesnil. In: Recherche sur la biologie de divers Diptères Endoparasites d' Orthoptères.- *Mem Mus Nat Hist Nat Ser A, Zool* **53**: 123-138; Paris / France.
- MACHLIS L, DODD P W D & FENTRESS J C [1985]: The pooling fallacy: problems arising when individuals contribute more than one observation to the data set.- *Z Tierpsych* **68**: 201-214; Hamburg & Berlin / Bundesrepublik Deutschland..
- MAGNHAGEN C [1991]: Predation risk as a cost of reproduction.- *Trends Ecol Evol* **6**: 183-186; Amsterdam / Nederland.
- ROBERT D, AMOROSO J & HOY R R [1992]: The evolutionary convergence of hearing in a parasitoid fly and its cricket host.- *Science* **258**: 1135-1137; Washington / USA.
- ROBERT D, READ M P & HOY R R [1994]: The tympanal hearing organ of the parasitoid fly *Ormia ochracea*.- *Cell & Tissue Res* **275**: 63-78; Heidelberg / Bundesrepublik Deutschland..
- RYAN M J & KEDDY-HECTOR A [1992]: Directional patterns of female mate choice and the role of sensory biases.- *Am Nat* **139**: S4-S35; Chicago / USA.
- SEARCY W A & ANDERSSON M [1986]: Sexual selection and the evolution of song.- *Annu Rev Ecol Syst* **17**: 507-533; Palo Alto / USA.
- STEPHENS D W & KREBS J R [1986]: *Foraging theory*.- Princeton University Press; Princeton / USA.
- WAGNER W E [1995]: Convergent song preferences between female field crickets and acoustically orienting parasitoid flies.- *Behav Ecol* **7**: 279-285; Oxford / USA.
- WALKER T J [1993]: Phonotaxis in female *Ormia ochracea* (Diptera: Tachinidae), a parasitoid of field crickets.- *J Insect Behav* **6**: 389-410; Kansas / USA.
- ZUK M & KOLLURU G R [1998]: Exploitation of sexual signals by predators and parasitoids.- *Q Rev Biol* **73**: 415-438; Chicago / USA.
- ZUK M, SIMMONS L W & CUPP L [1993]: Calling characteristics of parasitized and unparasitized populations of the field cricket *Teleogryllus oceanicus*.- *Behav Ecol Sociobiol* **33**: 339-343; Heidelberg / Bundesrepublik Deutschland..

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