

When to give up responding acoustically in *Poecilimon* bush-crickets: a clue to population density

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Abstract

Acoustic communication systems with the purpose to find a mate are in the simplest case formed by one partner (usually the male) singing and one partner (usually the female) recognizing the signal and approaching the sender phonotactically. In some bush-cricket families, however, more complex acoustical communication systems evolved with the females producing response songs. In such a system the phonotactic approach has not to be done alone by the female. Both sexes may move towards each other or the male has to take the risky approach. Yet surprisingly this flexible system was given up several times independently, and the species returned to the unidirectional system with singing males and moving females.

To understand the reasons of this reduction we studied the mating behaviour of a species with bi-directional system, *Poecilimon affinis*, in the field. Within this genus, the acoustical female response behaviour has been lost at least three times independently. To imitate the effect of a reduction, we produced mute females (by cutting off one tegmen). In a comparison of the female mating frequency, there was no difference in a population at high density – ca. 40% of both types of females mated per night, but a highly significant difference at low density (37% intact to 5% mute). These results indicate that in species evolving at high densities the costs of responding may be not balanced by advantages, at least if these are measured in the number of matings (and obtained spermatophores).

Zusammenfassung

Bei vielen Insekten besteht die Hauptfunktion eines akustischen Kommunikationssystems darin, das Zusammenfinden von Männchen und Weibchen zu gewährleisten. Im häufigsten und einfachsten Fall produziert das Männchen den Gesang, und das Weibchen findet es phonotaktisch. In einigen Laubheuschrecken-Gruppen sind jedoch kompliziertere Systeme entstanden, in denen die Weibchen Antwortgesänge produzieren. Hier muss nicht unbedingt das Weibchen zum Männchen hinlaufen - es können sich auch beide Geschlechter duettierend aufeinander zu bewegen oder das Männchen muss zusätzlich zum Singen auch noch die ebenfalls gefährliche Annäherung allein übernehmen. Erstaunlicherweise wurde dieses flexible System aber mehrfach unabhängig aufgegeben, und die Arten kehrten zum unidirektionalen System zurück. Um diese Reduktion der Weibchen-Antwort zu verstehen, haben wir das Paarungsverhalten einer Art mit bidirektionalem System, *Poecilimon affinis*, untersucht. Innerhalb dieser Gattung wurde die Weibchenantwort mindestens dreimal unabhängig auf-

gegeben. Um den Verlust des Weibchen-Antwortens zu imitieren, haben wir künstlich stumme Weibchen erzeugt (durch Abschneiden eines Vorderflügels). In einem Vergleich der Paarungshäufigkeit dieser stummen Weibchen mit der von intakten Weibchen zeigte sich, dass bei hohen Populationsdichte keine Unterschiede zu beobachten waren (ca. 40% aller Weibchen paarten sich jede Nacht). Bei niedriger Populationsdichte traten dagegen sehr deutliche Unterschiede auf (37% intakt gegen 5% stumm). Diese Ergebnisse zeigen, dass bei hoher Populationsdichte die Kosten des Weibchen-Antwortens vermutlich nicht durch Vorteile ausgeglichen werden, jedenfalls wenn man die Vorteile abschätzt durch die Anzahl der Paarungen (und der dabei erhaltenen Spermatophoren).

Introduction

Acoustic communication systems used for mate finding are in the simplest case formed by one partner (usually the male) singing and one partner (usually the female) recognizing the signal and approaching the sender phonotactically (for a review see EWING 1989). Such systems are typical for crickets (Grylloidea) and most bush-crickets (Tettigoniodea). The males produce long-lasting songs and the females ready to mate approach. Here the males carry the risk to be attacked by acoustically orienting predators or parasitoids, while the mute females have to be aware of predators specialised in movement detection.

In the tettigonioid families Phaneropteridae and Bradyporidae, however, more complex acoustical communication systems independently evolved, with the females producing response songs (reviews ROBINSON 1990; ROBINSON & HALL 2002; BAILEY 2003, 2006). These duet systems are more flexible. Both sexes may move towards each other or – in the case of strong intraspecific male competition – the male has to take the risky approach alone in addition to his calling costs (HELLER 1992; BATEMAN 2001). In laboratory tests with several species of phaneropterids, SPOONER (1968) documented the variability of the system and found that often both sexes move. In some physiological experiments the male phonotactic behaviour was examined in detail (e.g. ROBINSON et al. 1986 for *Leptophyes punctatissima*, HELLER & HELVERSEN 1986 for some *Poecilimon* species).

Few field experiments or studies, however, were made exploring who – male or female – actually performs the phonotactic approach in such a bi-directional system and what will be the consequences for the mating success. Yet surprisingly this flexible system was lost several times independently in the Phaneropteridae by reducing the female stridulatory organs (e.g., CHOBANOV & HELLER 2010), and the species returned to the unidirectional system with singing males and moving females. Similar changes at a behavioural level are known from Bradyporidae, where the females in some (all?) species of the genus *Ephippiger* obviously never respond acoustically, although they have well developed stridulatory organs (see e.g. HARTLEY et al. 1974; DUIJM & OUDMAN 1983; RITCHIE 2000). In the ephippigerine *Steropleurus stalii* the females tend to reduce their phonotactic movements with each mating (BATEMAN 2001).

To get a better understanding of the behavioural flexibility and of possible reasons for a reversal we first tested, which sex would actually start with the phono-

tactic approach after a duet has begun in a species with bi-directional communication. In a second series of experiments we compared the mating frequency of intact and of artificially produced mute females under different population densities. The mute females represent the condition found in species after the loss of the stridulatory organs. Population density is known as an important factor influencing e.g. operational sex ratio (GWYNNE 1984) or female choosiness (LEHMANN 2007) in bush-crickets, is a key parameter in general models of sex-specific search roles (e.g. KOKKO & WONG 2007) and is assumed to be correlated with certain song patterns (e.g. HARTLEY et al. 1974). The importance of female acoustical response and phonotaxis was measured in terms of female mating success. For estimating mating frequency we took advantage of another peculiarity of the tettigoniid mating system. When after acoustical duetting both sexes have met, the male transfers a spermatophore to the female, where it can be observed for several hours. This nuptial gift represents an important nutritional resource for female bush-crickets in general (e.g. GWYNNE 2001; VAHED 1998; VOIGT et al. 2005, 2008) and in *Poecilimon* in special (e.g. REINHOLD & HELLER 1993; MCCARTNEY et al. 2009).

For the experiments we have chosen a species of the phaneropterid genus *Poecilimon*, *P. affinis*. The genus *Poecilimon* is the largest bush-cricket genus in the Palaearctic with at present 136 species (EADES et al. 2011). All species are micropterous, and the only function of the tegmina in males and females seems to be sound production. Already in 1886 (PUNGUR 1886) male and female stridulatory organs were described and figured for one of its species. Especially interesting is the unusually variable communication system. Within the genus, the acoustical female response behaviour has been lost several times independently (at least three times; see ULLRICH 2007, 2010; CHOBANOV & HELLER 2010). These reductions are recognisable by the complete loss of female tegmina including stridulatory organs.

Methods

The experiments were performed in the Vernon Mountains near Pisoderion (Northern Greece, N. Florina; 40°46'N, 21°14'E) from July 31st to August 17th 1988, some phonotaxis tests also in August 1989 and 1990. *Poecilimon affinis* occurs here mainly in the beech forest zone at altitudes of 700 to 1900 m a.s.l. The species is found in unwooded plots, especially in clearings held open by grazing sheep and goats. Typical are meadows with a large number of herbs (e.g. *Thymus*) and an additional sparse shrub-like vegetation of thistles, *Verbascum* and *Urtica*. *Poecilimon affinis* is a relative large, nearly exclusively phytophagous bush-cricket (mean body mass 2.1 g females, 1.4 g males), active mainly at night. Its mating behaviour was studied in the same area by HELLER & HELVERSEN (1991).

Onset of phonotaxis

For measuring the onset of phonotaxis, an acoustically responding female was placed on a thistle at a height of around 40 cm. At a distance of at maximum 10 m (less than the hearing range of both sexes; Helversen et al., in prep.) a male was sitting on a thistle at the same height. Start of a duet was defined by

the first female response, start of phonotaxis as that moment when one animal left its plant and moved in direction of the other. 12 out of 26 females were virgins which did not show any differences to the mated females in behaviour.

Mating frequencies at different densities in the field

Female mating frequency was measured at two different population densities. We choose two areas each about 2000 m². The area with the high population density (HD) was covered with thistles, *Urtica* and *Verbascum* at about 70%. It was similar in vegetation structure to that area in which the population density simultaneously was measured by marking all animals individually (HELLER & HELVERSEN 1991). The plot with the low density (LD) consisted mainly of short grass meadow covered with shrub-like vegetation only at about 10%. We estimated the male density in both areas based on number of observed and of singing males. In the area with low density all males we found (7) were included in the experiment (see below), at high density we estimated 10-20 males per 100 m² (similar as in HELLER & HELVERSEN 1991: 21-26 males/100 m²). In both areas we released females, captured in other areas or within the areas, which were marked individually by ink (metallic marker Pilot super color silver Extra fine) on the pronotum. In addition, they were marked with a small piece (ca. 2 x 4 mm²) of self-adhesive reflective tape at the tip of one hind femur (HELLER & HELVERSEN 1990). The tag of reflective tape makes it possible to detect and locate a marked animal at night from a distance of more than 100 m by using a head-lamp. So we could relocate the widely dispersed test females at each check with a probability of about 80-90%. In the HD area we released 60 females distributed over the whole area so that the natural ratio of males to females was not much influenced. In the LD area, where we released 28 females in addition to the 5 females found there, these animals would have changed the male to female ratio quite significantly. Therefore we released 20 marked males in addition and marked also all animals found in that area, resulting in 33 test females to 27 marked males (density 3 animals per 100 m²).

Before releasing, the marked females were randomly either left otherwise unchanged or made mute by cutting one tegmen or made deaf by destroying both tympanic organs (with a hot insect pin). The recapture rate was about the same for intact and mute animals, so the operation did not seem to affect the survival. Nevertheless, to exclude any effects of the operation, only such animals were included in the calculation which were alive at least in the third night after releasing. Surprisingly, in the HD area much less animals than in the LD area were relocated until the third day. Therefore finally data of 37 females from the HD area and of 33 females from the LD area were evaluated.

During the whole observation period of 11 days (2 to 11 August 1988) during every night two checks were made in both areas, the first between 11 p.m. and 0.30 a.m. and the second between 4.30 and 6.00 a.m., just before dawn. During the check we noted for each individually marked female if it was carrying a spermatophore or not. Around 50% of the females observed with a spermatophore during the first check were still carrying it 4 to 6 hours later during the second check. So probably we missed only few matings due to too fast feeding. In any case, this potential error would not disturb our comparison because both groups

of females would be similarly affected. The same is true if the animals should also mate during day-time. Statistics were calculated using LANGSRUD (2011) and KIRKMAN (1996).

Results

Onset of phonotaxis

The probability that an animal becomes phonotactically active depends on its actual individual motivation to mate, which is influenced by age, time since last mating etc. To keep these variables constant we used only animals ready to mate – males that had not mated for at least three days and that were singing at a high rate, females that responded to at least 70% (mostly to more than 90%) of male songs.

70% of the males tested had started moving towards the females already after 6 minutes, while nearly 80% of the females still sat on their plants even after 30 min (Fig 1; after 30 min male-female difference $p > 0.001$; Fisher's Exact Test). Typically the females moved slightly orienting towards the males and positioned themselves more exposed, but did not leave their place. According to few experiments that lasted for more than 30 min (unpublished data) the females remained even considerably more than half an hour. The fastest males started after having heard five female responses (median of 11 males), while some females had responded with a high rate to more than 360 male songs without leaving their plants.

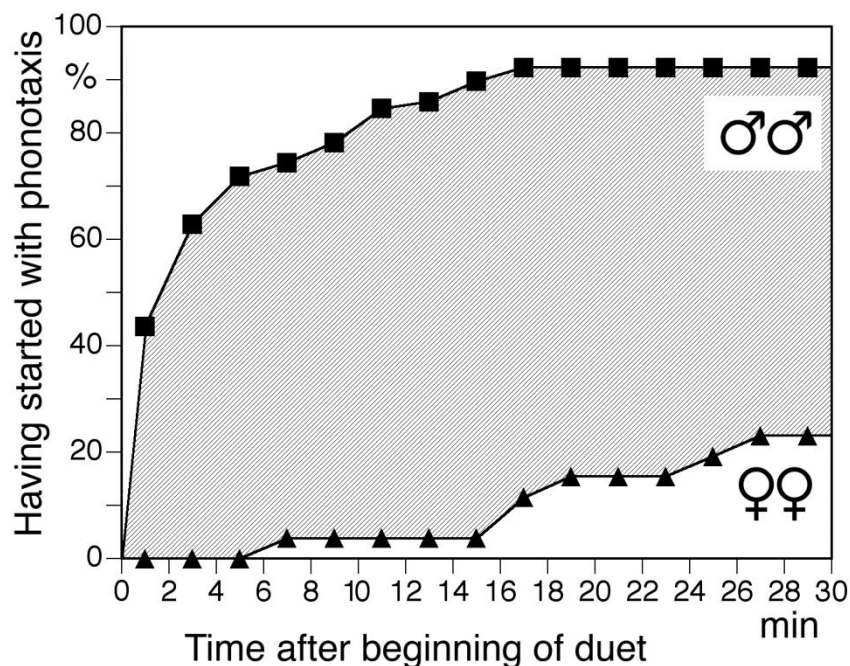


Fig. 1: Sex specific frequency of phonotaxis after the beginning of a duet (n = 87 males, 26 females).

Female mating frequency

Obviously our female manipulations had effects on the mating frequency (separate tests for HD and LD populations: $P > 0.001$; exact contingency table tests), but not the same at high and low population density. During the observation period we registered a high mating frequency of intact females in both HD and LD population (Fig. 2). The data indicate that intact females obtained the same typical mating frequency at high and low densities ($p = 0.61$; Fisher's Exact Test). These percentages are very similar to that observed in a high density population closely nearby (HELLER AND HELVERSEN 1991), where all animals were marked individually.

The mating frequency of mute females, however, differed significantly in both areas (Fig. 2). At high density the females mated with about the same rate as intact females (HD and LD combined; $p = 0.56$; Fisher's Exact Test). At low density the mating frequency was much lower (Fig. 2; $p < 0.001$; Fisher's Exact Test). Here it did not differ from that of deaf females (HD and LD combined; $p = 1$; Fisher's Exact Test).

The mating frequency of deaf females who are not able to hear a male song nor able to respond to was very low. In each of both areas we observed only one mated deaf female ($p = 1$; Fisher's Exact Test). These data are not essential for our comparison and we cannot exclude effects of the deafening operation on the motility. However, the results confirm the data of the mute females.

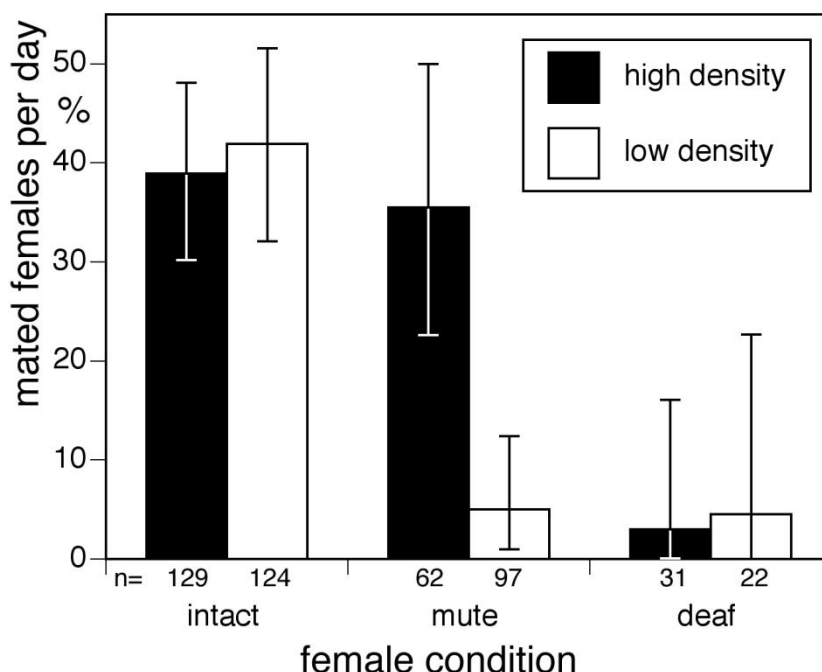


Fig. 2: Mating frequency (mating frequency per day) of the experimental females; error bars 95% confidence intervals.

Discussion

With the first part of our experiments we demonstrate that females of *P. affinis* are typically quite reluctant to approach a calling male phonotactically. They prefer to respond acoustically, while the males are eager to use the female signals as guide during their approach. Nearly all males started their phonotactic approach within 20 min after the onset of an acoustical duet, whereas only a much lower percentage of females did so. This result correlates with the observed mating frequencies at various densities. Mute females were not successful in obtaining matings, but surprisingly only at low population densities. At high density, however, mute females are obviously able to approach males and to obtain matings (and spermatophores) nearly as efficiently as intact females. This behavioural flexibility seems to be pre-programmed, with switching from acoustic to phonotactic response perhaps triggered by duration of waiting time. The intensity of the male signal could be another factor involved. Females may be more inclined to a phonotactic approach if the perceived signal is loud, indicating close proximity of the sender and therefore only a short moving effort. Since our phonotaxis experiments were done during day-time, but mating occurs at night, we can also not exclude the possibility that females are less reluctant to move in the night-time. The idea that the mute females might eavesdropping acoustical responses of other females and try to intercept approaching males seems less plausible, since female signals are much softer than those of males (Helvesen et al., in prep.) and the path of approaching males is difficult to predict.

At low population density, neither mute nor deaf females were able to obtain many matings. The few spermatophores observed in such females may have been the result of meetings by chance without previous acoustical contacts. As can be seen from the high mating rate of mute females at high density, female song per se is not important. In contrast to e.g. duetting acridids (KRIEGBAUM 1989), both male and female stop singing after having made physical contact (see HELLER 2006). Obviously (mute) female phonotaxis did not work under that conditions. Reasons may be found either within male behaviour – males may leave their position unaware that a female is approaching or may call too rarely to be tracked over a long time. Or the female does not start her phonotactic approach if the perceived male signal is too soft. Such a behaviour should be adaptive if the risks during phonotaxis are not outweighed by the benefits of an increased mating rate. Our results are also in line with a recent model (MCCARTNEY et al., in press.) that demonstrates that search roles can reverse when multiple mating brings about sufficiently benefits to females.

Although population density has often not explicitly mentioned while discussing the evolution of insect acoustic communication (e.g., EWING 1989; BAILEY 1990; but see HARTLEY et al. 1974), it seems quite important at least in phaneropterids. On a world-wide scale many phaneropterid bush-crickets are long-winged and known as good flyers. For such species a bi-directional communication is very efficient, because a male can search large areas for responding females by a combination of singing and flying (e.g., HELLER et al. 1997). The species are thus able to exist at quite low densities. If species become flightless (as *Poecilimon*

and other genera of Barbitistini; HELLER 1990), they lose much of the advantages of bi-directionality and the population density must increase. However, an exchange of information about the location of the partners is still useful at densities low for the respective species. Our results indicate that for species adapted to live at high-densities for whatever reasons (could be e.g. feeding on first succession plants growing after forest-fires) uni-directional communication may probably be sufficient. Under high density and high competition the females do not need to spend energy for wings and muscles and have more space for eggs (compare BAILEY & KAMIEN 2001). Under the same conditions the males may have to produce songs, which can be localised by the females more easily (HELLER & HELVERSEN 1993), but they have to carry the increased risks from predators (HELLER 1992) and parasitoids (LEHMANN & HELLER 1998, LEHMANN et al. 2001) resulting in high costs for the parasitized males (LEHMANN & LEHMANN 2000). It will be interesting to look for the ecological factors characterising those species that can be assumed to have evolved at high densities.

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References

- BAILEY, W.J. (2003): Insect duets: Underlying mechanisms and their evolution. - *Physiol. Entomol.* 28: 157-174.
- BAILEY, W.J. (2006): Insect songs - the evolution of signal complexity. - In: *Insect Sounds and Communication: Physiology, Behaviour, Ecology and Evolution* (DROSOPOULOS, S. & CLARIDGE, M. F., eds.). Taylor & Francis, Boca Raton, London & New York: 127-136.
- BAILEY, W.J. & KAMIEN, D. (2001): Hearing dimorphism, trait variation and conflicts over space in the thorax of the bushcricket *Requena verticalis* (Listroscolidinae: Tettigoniidae: Orthoptera). - *J. Comp. Physiol. A* 187: 647-652.

- BATEMAN, P.W. (2001): Changes in phonotactic behavior of a bushcricket with mating history. - *J. Insect Behav.* 14: 333-343.
- CHOBANOV, D.P. & HELLER, K.-G. (2010): Revision of the *Poecilimon ornatus* group (Orthoptera: Phaneropteridae) with particular reference to the taxa in Bulgaria and Macedonia. - *Eur. J. Entomol.* 107: 647-672.
- DUIJM, M. & OUDMAN, L. (1983): Interspecific mating in *Ephippiger* (Orthoptera, Tettigoniodea). - *Tijdschr. Entomol.* 126: 97-108.
- EADES, D.C., OTTE, D., CIGLIANO, M.M. & BRAUN, H. (2011): Orthoptera Species File Online. Version 2.0/4.0. <http://Orthoptera.SpeciesFile.org>. - Accessed 05 March 2011.
- EWING, A.W. (1989): *Arthropod bioacoustics. Neurobiology and behaviour.* - Edinburgh University Press, Edinburgh. 260pp.
- GWYNNE, D.T. (1984): Sexual selection and sexual differences in mormon crickets (Orthoptera Tettigoniidae *Anabrus simplex*). - *Evolution* 38: 1011-1022.
- GWYNNE, D.T. (2001): *Katydids and bush-crickets: reproductive behavior and evolution of the Tettigoniidae.* - Cornell University Press, New York.
- HARTLEY, J.C., ROBINSON, D.J. & WARNE, A.C. (1974): Female response song in the Ephippigerines *Steropleurus stali* and *Platystolus obvius* (Orthoptera, Tettigoniidae). - *Anim. Behav.* 22: 382-389.
- HELLER, K.-G. (1990): Evolution of song pattern in East Mediterranean Phaneropteridae: Constraints by the communication system. - In: *The Tettigoniidae: Biology, Systematics and Evolution* (BAILEY, W.J. & RENTZ, D. C. F., eds). Springer, Berlin et al.: 130–151.
- HELLER, K.-G. (1992): Risk shift between males and females in the pair-forming behavior of bushcrickets. - *Naturwissenschaften* 79: 89–91.
- HELLER, K.-G. (2006): Song evolution and speciation in bushcrickets. - In: *Insect Sounds and Communication: Physiology, Behaviour, Ecology and Evolution* (DROSOPOULOS, S. & CLARIDGE, M.F., eds.). Taylor & Francis, Boca Raton, London & New York: 137-151.
- HELLER, K.-G. & HELVERSEN, D. V. (1986): Acoustic communication in phaneropterid bushcrickets: species-specific delay of female stridulatory response and matching male sensory time window. - *Behav. Ecol. Sociobiol.* 18: 189-198.
- HELLER, K.-G. & HELVERSEN, D. V. (1991): Operational sex ratio and individual mating frequencies in two bushcricket species (Orthoptera Tettigoniodea *Poecilimon*). - *Ethology* 89: 211-228.
- HELLER, K.-G. & HELVERSEN, D. V. (1993): Calling behavior in bushcrickets of the genus *Poecilimon* with differing communication systems (Orthoptera: Tettigoniodea: Phaneropteridae). - *J. Insect Behav.* 6: 361-377.
- HELLER, K.-G. & HELVERSEN, O. V. (1990): Survival of a phaneropterid bush cricket studied by a new marking technique (Orthoptera: Phaneropteridae). - *Entomol. Gen.* 15: 203-208.
- HELLER, K.-G., SCHUL, J. & INGRISCH, S. (1997): Sex-specific differences in song frequency and hearing in some duetting bushcrickets (Orthoptera: Tettigoniodea: Phaneropteridae). - *Zool. Anal. Complex Syst.* 100: 110-118.
- KIRKMAN, T. W. (1996): *Statistics to Use.* <http://www.physics.csbsju.edu/stats/>. - Accessed 07.10.2011.
- KOKKO, H. & WONG, B.B.M. (2007): What determines sex roles in mate searching? - *Evolution* 61: 1162-1175.
- KRIEGBAUM, H. (1989): Female choice in the grasshopper *Chorthippus biguttulus*. Mating success is related to song characteristics of the male. - *Naturwissenschaften* 76: 81-82.
- LANGSRUD, O. (2011): <http://www.langsrud.com/stat/Fishertest.htm>. - Accessed 07.10.2011.

- LEHMANN, G. (2007): Density-dependent plasticity of sequential mate choice in a bushcricket (Orthoptera: Tettigoniidae). - Austral. J. Zool. 55: 123-130.
- 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.
- LEHMANN, G.U.C, HELLER, K.-G. & LEHMANN, A.W. (2001): Male bushcrickets favoured by parasitoid flies when acoustically more attractive for conspecific females (Orthoptera: Phanopteridae / Diptera: Tachinidae). - Entomol. Gen. 25: 135-140.
- LEHMANN, G.U.C. & LEHMANN, A. (2000): Spermatophore characteristics in bushcrickets vary with parasitism and remating interval. - Behav. Ecol. Sociobiol. 47: 393-399.
- MCCARTNEY, J., KOKKO, H., HELLER, K.-G. & GWYNNE, D.T. (in press) The evolution of sex differences in mate searching when females benefit: new theory and a comparative test. - Proc. R. Soc. Biol. Sci. B, published online 28 September 2011; doi: 10.1098/rspb.2011.1505
- MCCARTNEY, J., POTTER M.A., ROBERTSON, A.W., TELSCHER, K., LEHMANN, G.U.C., LEHMANN, A., HELVERSEN, D. V., REINHOLD, K., ACHMANN, R. & HELLER, K.-G. (2009): Understanding nuptial gift size in bush-cricket: an analysis of the genus *Poecilimon* (Tettigoniidae: Orthoptera). - J. Orthoptera Res. 17: 231-242.
- PUNGUR, J. (1886): Beiträge zur Naturgeschichte einer wenig bekannten Laubheuschreckenart. Mathematische und Naturwissenschaftliche Berichte aus Ungarn 4: 78-85, pl. II-III.
- REINHOLD, K. & HELLER, K.-G. (1993): The ultimate function of nuptial feeding in the bushcricket *Poecilimon veluchianus* (Orthoptera: Tettigoniidae: Phaneropterinae). - Behav. Ecol. Sociobiol. 32: 55-60.
- RITCHIE, M.G. (2000): The inheritance of female preference functions in a mate recognition system. - Proc. R. Soc. Biol. Sci. B 267: 327-332.
- ROBINSON, D.J. (1990): Acoustic communication between the sexes in bushcrickets. - In: The Tettigoniidae: Biology, Systematics and Evolution (BAILEY, W.J. & RENTZ, D.C.F., eds). Springer, Berlin et al.: 112-129.
- ROBINSON, D.J. & HALL, M.J. (2002): Sound signalling in Orthoptera. - Adv. Insect Physiol. 29: 151-278.
- ROBINSON, D.J., RHEINLAENDER, J. & HARTLEY, J.C. (1986): Temporal parameters of male female sound communication in *Leptophyes punctatissima*. - Physiol. Entomol. 11: 317-324.
- SPOONER, J.D. (1968): Pair-forming acoustic systems of phaneropterine katydids (Orthoptera, Tettigoniidae). - Anim. Behav. 16: 197-212.
- ULLRICH, B. (2007): Phylogeny of the bush cricket genus *Poecilimon* Fischer, 1853 (Orthoptera: Phaneropteridae) inferred from mitochondrial and nuclear markers. - Dissertation. University of Bielefeld.
- ULLRICH, B., REINHOLD, K., NIEHUIS, O. & MISOF, B. (2010): Secondary structure and phylogenetic analysis of the internal transcribed spacers 1 and 2 of bush crickets (Orthoptera: Tettigoniidae: Barbitistini). - J. Zool. Syst. Evol. Res. 48: 219-228.
- VAHED, K. (1998): The function of nuptial feeding in insects: A review of empirical studies. - Biol. Rev. 73: 43-78.
- VOIGT, C.C., KRETZSCHMAR, A., SPEAKMAN, S., JOHN, R. & LEHMANN, G.U.C. (2008): Female bushcrickets fuel their metabolism with male nuptial gifts. - Biol. Lett. 4: 476-478.
- VOIGT, C.C., MICHENER, R. & KUNZ, T.H. (2005): The energetics of trading nuptial gifts for copulations in katydids. - Physiol. Biochem. Zool. 78: 417-423.