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Acoustic communication in Phaneropterinae (Tettigoniodea) – a global review with some new data

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Abstract

Phaneropterinae is the largest subfamily within the bush-crickets/katyids (Tettigoniodea), with about 2451 species, and with a world-wide distribution. Its acoustic communication differs from all other tettigonioid groups in that females primarily and typically respond to the male calling song with their own acoustic reply, a behaviour referred to as duetting. This type of response seems to have been lost only in a few species with wingless females.

According to our literature review, information about the song patterns of about 330 species of Phaneropterinae have been published world-wide. Included in this number are *ca* 170 species of Barbitistini, a flightless West Palearctic tribe, which are treated separately. In the present study we summarize information from the above 330 species. We examine the morphology of stridulatory and hearing organs, and analyze the acoustic signals for frequency, number of syllables and number of interval types. We also have examined if and how responding by sound may have influenced other aspects of the acoustic communication system, especially the structure of the male calling song.

Overall, the songs of male Phaneropterinae are similar to those of other tettigonioids. However, some Phaneropterinae species with very long and complex songs are found on all continents, exceeding in these characters nearly all other Ensifera species. These songs contain several different types of syllables and intervals of various duration. Because of this high interspecific variability (reaching from very simple to extremely complex), male phaneropterine songs are by far more variable than those of other tettigonioid families.

However, since there are so few data on the behaviour of most Phaneropterinae species, and especially for females, we still are limited in our understanding of the reasons behind the song variability. Sexual selection by females choosing to respond preferentially to certain song types could be an important evolutionary force, but probably only in combination with some unknown ecological and behavioural factors.

Key words

katydid, mating, courtship, sexual behavior, female response, duetting, amplitude modulation, carrier frequency

Introduction

The subfamily Phaneropterinae is a large (2451 valid species; OSFO 2014/11/05), diverse, but also distinct group of bush-crickets (katyids; Tettigoniodea). Due to the large number of species, it has attracted the attention of taxonomists, resulting in the first world-wide revision of any tettigonioid group (Brunner von Wattenwyl, 1878). Later, however, a rapid increase in the number of new described species prevented further general revisions, and subsequent comprehensive treatments of the phaneropterine fauna were restricted to selected areas or countries, such as the USSR by Bey-Bienko (1954)

or China by Kang *et al.* (2014). Recent molecular studies support the monophyly of the group (Mugleston *et al.* 2013) as defined by older authorities. By some authors, Phaneropterinae *s.str.* is now considered as one of four subfamilies of Phaneropteridae (Heller *et al.* 2014).

Morphologically, many phaneropterines can easily be recognised by the length of the hind wings, which surpass the forewings. While this character is not found in all species and is also shared by some species from other groups, the shape of the eggs seems to be diagnostic. As already described and figured by Bey-Bienko (1954), the eggs of all species studied so far are flat [for one remarkable modification see Massa (2013)], probably adapted for oviposition into plant tissues. Corresponding to egg shape and oviposition site, the ovipositor is usually strongly laterally compressed. Together with the closely related Pseudophyllinae and Mecopodinae (Gorochov 1995, Mugleston *et al.* 2013), all species feed nearly exclusively on plants (Rentz 2010), contrasting with the more omnivorous or even purely carnivorous habit of most other tettigonioids.

Phaneropterinae are characterized not only in hind wing length, egg shape, oviposition and feeding behaviour, but also in communication. Like most tettigonioids, they communicate by sound. However, unlike most other tettigonioid groups, female phaneropterines respond to the male calling song with their own acoustic reply, thus initiating a duet. Only in very few genera has this female behaviour been secondarily lost, together with the sound producing organs (some species in *Poecilimon* Fischer, 1853, *Odontura* Rambur, 1839, *Odonturoides* Ragge, 1980, *Arachmitus* Hebard, 1932; see *e.g.*, Helversen *et al.* 2012, Strauß *et al.* 2014). This duetting behaviour has long been known. The female sounds seem to have been first heard and described by Riley (1874 *vide* Spooner 1968), while the female sound producing organs were discovered by Pungúr (1886). At the end of the last century several reviews about Phaneropterinae communication were produced (Zhantiev & Korsunovskaya 1986, Spooner 1995), but based mainly on geographically restricted data and focusing on selected aspects.

Acoustical answering is not uncommon among insects communicating by sound, but among tettigonioids outside Phaneropterinae it is known only in some species of Bradyporidae (see Bailey 2003, Drosopoulou and Claridge 2006). At this time, we do not know the behavioral, ecological, and evolutionary consequences of such duetting. Nor do we know if duetting behaviour has influenced morphology, sound production, hearing and behaviour in phaneropterines.

Some North American phaneropterines possess extremely complex songs (Walker & Dew 1972, Walker *et al.* 2003, Walker 2004).

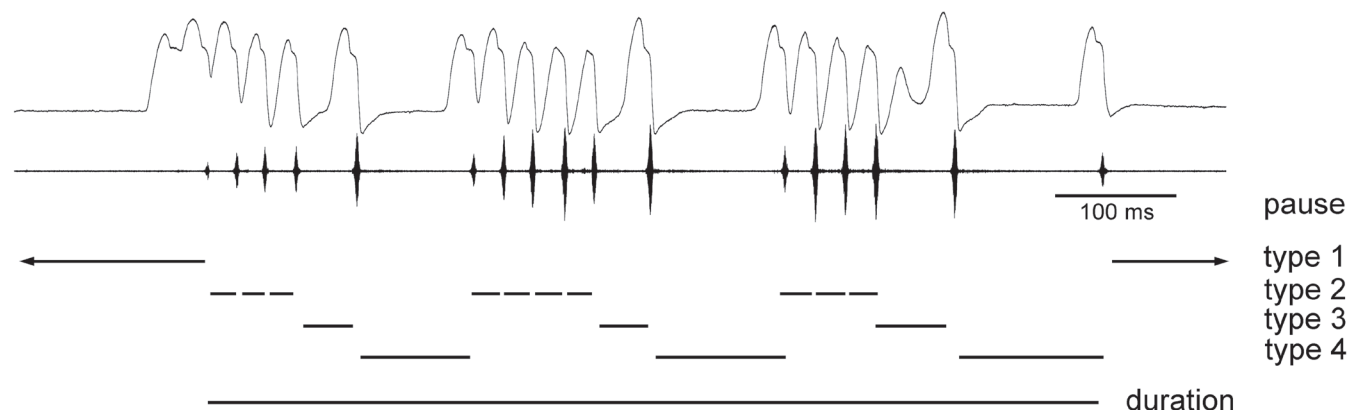


Fig. 1. Unit of male calling song of *Barbitites yersini* as example of a song with one syllable type, four pause types, 17 syllables and a duration of 750 ms. Oscillograms of stridulatory movement and song [synchronous registration of left tegmen movement and sound (upper line: upward deflection represents opening, downward closing; lower line: sound)]. See Stumpner & Meyer 2001 for details of the function of the pause types.

Walker (2004) assumed such complexity evolved from complexity of context; *i.e.*, duetting, including complex exchange of information about the mating partner, and possible eavesdropping selected for song complexity. But is this true for most or only a few species? For any comparison with other groups we are severely restricted because compiled data about tettigoniid acoustics do not exist. An additional complication is that we know little about mate-location behavior in Phaneropterinae: Does the male approach the stationary female or vice-versa? At what point do individuals switch from acoustic orientation to visual, chemical, tactile, or vibrational orientation? Do individuals alter song characteristics with distance from mate, intra-specific competition, or current predator threat? Until we know more about current and ancestral contexts, it is difficult to answer questions about why.

The first step in understanding acoustic communication in phaneropterines is analysis of their acoustics. However, comparing complex songs is not easy, and parameters of interest to the researchers may change with time. In this review we will therefore give tables with some basic information about the song of each species so that researchers can compare their data. We wish to present an overview of what is known about the acoustics of the different species of Phaneropterinae, treat the morphology of the organs for sound production and hearing, and also discuss data from hearing physiology and duetting behaviour. The main aspect, however, will be a comparative study of the male songs. Female replies will also be covered, but they seem to be much simpler in structure than male songs, and, unfortunately, much less known.

Methods

For this review, we evaluated all data about phaneropterine songs that we could find from the literature, CDs, and the internet site SINA; see detailed data in Supplementary Material SM1 and SM2. However, typically only one or a few sources per species are given (for older data see Heller 1988, Ragge & Reynolds 1998, SINA). In addition, we present new detailed data for the following species: *Ectadia fulva* Brunner von Wattenwyl, 1893 (THAILAND: Chiang Mai Prov., Doi Suthep (-Pui) (18°48'N, 98°55'E), 1100-1150 m, 13 iv 1995, leg. S. Ingrisch), *Monticolaria kilimanjarica* Sjöstedt, 1909 (TANZANIA: Mt. Kilimanjaro, 6 xii 2012, leg. Claudia Hemp; recording methods see Heller *et al.* 2010) and *Ectadia* sp. (CHINA: Yunnan, Honghe, Pingbian, Daweishan Forest Reserve (22°54'N,

103°41'E), 1700-2100 m, 15-17 viii 2013, leg. Liu Chunxiang). For the tables (SM1 and SM2) and calculations, we have also used some unpublished sound information from the specimens listed in the Supplementary Material SM3. For the authors of the scientific names see OSFO.

For definitions of terms used in insect acoustic analysis, consult Ewing (1989), Huber *et al.* (1989), Bailey (1991) or Ragge and Reynolds (1998).

In this review we compared the carrier frequencies (peak) and several parameters of the temporal pattern, including:

(1) Number of different syllable types. During one cycle of movement (opening and closing of the tegmina) an individual produces one syllable (see Ragge & Reynolds 1998). Using different movement patterns an animal can produce different syllable types. The wing stridulatory movements of many species have been studied (see Heller 1988). Where it is unknown, we have tried to get as correct an estimate as obtainable from the sound pattern. There are, however, a few species where the stridulatory movement is so complicated that the term syllable would be misleading compared to 'normal' species (*e.g.*, species of *Acrometopa* Fieber, 1853, of *Isophya* Brunner von Wattenwyl, 1878, and of *Ectadia fulva*). In these cases we have described clearly separated acoustical units as syllables.

(2) Number of pause types (see Fig. 1). By using several types of pauses between the syllables an animal is able to produce complicated, species-specific songs.

(3) Number of syllables per unit. In all species, after some time the same pattern of syllables and pauses is repeated. As a measure of song complexity, we counted how many syllables were contained in one unit of the song (before the next repetition starts). Here, problems can arise if identical subunits are repeated several times and it is unclear how many constitute a basic unit, and if one or several subunits are necessary for recognition by the receiving insect.

(4) Duration of song. We measured the duration of one unit from beginning of the first to end of the last syllable. All data refer to the period of activity only. Long intervals when the animal does not sing are excluded.

The male song pattern is known in 325 phaneropterine species, among them 164 members of the West Palearctic tribe Barbitistini. This group (269 recognized species; OSFO) differs from most other phaneropterines as they are micropterous and unable to fly. Since this character may influence the acoustic communication and is obviously over-represented in our sample, both groups (Barbitistini

and 'typical' Phaneropterinae) were analysed separately. 'Typical' Phaneropterinae include some species with different degrees of wing reduction outside Barbitistini.

Results

Morphology

Male stridulatory organs.—In phaneropterines, as in all tettigonioids, the male stridulatory file is situated on the underside of the left tegmen (Fig. 7B), and a scraper at the inner (anal) edge of the right tegmen (see e.g., fig. 3 in Heller & Helversen 1986). Stridulatory files are now often figured in revisions or descriptions of new species since they are often species-specific and useful for determination. However, normally it is impossible to make any predictions about the song from knowledge of the file. Therefore we will not give a list of species for which file data or figures are available. Concerning teeth number, phaneropterines are quite variable. The lowest number seems to be found in *Elimaia rosea* Brunner von Wattenwyl, 1878 which has only 12 (range = 10–14) teeth (Ingrisch 2011), while the highest numbers (up to 380) are found in some species of the genus *Hemielimaia* Brunner von Wattenwyl, 1878 (Ingrisch & Gorochov 2007). Closely related species with the same teeth number can produce quite different songs (e.g., Walker *et al.* 2003).

Unlike in most other tettigonioids, phaneropterine files often show abrupt changes in tooth size or tooth density (e.g., Leroy 1970). If the song – or better, the stridulatory movement – is known, it is often easy to understand the function of the irregularities, but not in advance. In *Acrometopa*, for example, the large teeth are used for the production of the louder part of the song only (see Figs 7, 8 and Heller 1988 for other examples).

The inner dorsal edge of the right tegmen serves as a scraper or plectrum (see fig. 1 in Heller 1988 for a scanning electron microscope photo), and scrapes along the file to produce the wing vibrations that generate the acoustic signal. The right tegmen also contains the mirror, veins and/or other resonating structures that help determine the frequency spectrum of the song (see e.g., fig. 2 in Heller & Hemp 2014; Fig. 2A). These structures are typically confined to the dorsal field of the tegmen, an area close to the articulation. Only in males of some species of the genus *Oxyecous* are large parts of the right tegmen swollen, transparent, and mirror-like (Ragge 1956; Fig. 2C) and may function in sound radiation. Precursors of such swollen tegmina seem to exist in *Melidia* species (Fig. 2A; see

photos in OSFO) and *Ducetia punctipennis* (Gerstaecker, 1869) (Fig. 2B; see note in Ragge 1961 and photos in OSFO). Also in species without a clearly defined mirror (e.g., *Horatosphaga leggei*; see Heller *et al.* 2014) other parts of the tegmina may resonate.

Female stridulatory organs.—Unlike in most other Tettigoniodea, female phaneropterines also usually possess tegminal stridulatory organs. Their morphology differs from that of males. The female stridulatory organs were discovered and figured by Pungúr (1886) in a species of *Poecilimon*. In all phaneropterines studied thus far, the teeth are spine-like and found on the upper side of the right tegmen, and the scraper is often formed by the inner (anal) edge of the left tegmen. The number of teeth and also the number of stridulatory veins varies greatly in females, and is mostly not species-specific. In *Holochlora nigrotympana* Ingrisch, 1990, for example, high numbers of teeth and veins are easily visible (fig. 1 in Heller *et al.* 1997b), whereas the low numbers (10–15 small teeth on one vein) in *Nanoleptopoda* Braun, 2011 are even difficult to detect (Braun 2011). A second scraper system is known only in some Barbitistini. Here an elevated vein acting as scraper crosses the lower side of the right tegmen (see figures in Heller & Helversen 1986, Zhantiev & Korsunovskaya 1986).

Hearing organs.—In males and females the auditory sensory cells are combined in complex organs (Montealegre-Z *et al.* 2012, Palghat *et al.* 2012), one in each fore tibia, situated just below the femur-tibia articulation. Each organ has two tympanic membranes, one on each side of the leg. These membranes are exposed both to sound coming directly from the outside, and to acoustic input coming from the prothoracic spiracle reaching the tympana from the inner side via the auditory trachea. In this general aspect the Phaneropterinae do not differ from other bush-crickets. However, in most Phaneropterinae the thoracic auditory spiracles and bullae (entrance of the auditory trachea) are extraordinarily large, larger than in any other tettigoniid group (Bailey 1990). Although large in both sexes, they are often larger in males than in females (Bailey 1990). The sound coming through the thorax is thought to be dominant over that of sound impinging directly on the external surface of the tympanic membrane (e.g., Michelsen *et al.* 1994). Comparative physiological measurements in Barbitistini support the hypothesis that large bullae increase the sensitivity, at least for high frequencies above 10 to 15 kHz (Stumpner & Heller 1992, Strauß *et al.* 2014), even in this short-winged tribe, where the bullae are relatively small compared



Fig. 2. Left and right male tegmina in species that have both a distinct mirror on the right tegmen (near base of wing), and also a transparent mirror-like area, outside the mirror, on the right tegmen. A) *Melidia laminata* B) *Ducetia punctipennis*; C) *Oxyecous apertus*. Scale 5 mm.

to most long-winged species.

There is a large variety in size and shape of cuticular folds around the tympana. In many phaneropterines the tympanic membranes are completely open or 'naked', meaning that there are no cuticular ridges shielding or covering part of the membrane. In others species, one side (the anterior) is covered by a cuticular fold of different size, and yet in other species the membranes of both sides are behind cuticular folds or walls (Bailey 1990). The possession of these folds is used to define some tribes; asymmetric ears are characteristic for the mainly Asian Holochlorini and the African Poreuomenini. At present, there is no evidence of an acoustic function of the folds, especially not in the low-frequency range where the input through the tympana may be most important (see below). Here the wavelengths are much larger than the folds. Possibly the folds offer some mechanical protection of the tympanic membranes. In *Oxyecous lesnei* Chopard, 1936, the asymmetric fold is much larger in the male than in the female, but the reason is unknown (Ragge 1956, Bailey 1990).

Sounds and hearing

Although both male and female phaneropterines can usually produce sounds via wing stridulation, only the male's sound is referred to as a calling song. When characterizing and comparing various calling songs, two different aspects of the sound should be considered separately: 1) A song may have different carrier frequencies, which may activate different sensory cells (spectral properties; frequency domain analysis), and/or 2) a song may have different amplitude modulations, evaluated by the central nervous system (time domain analysis). Whether or not the songs of males and females and of different species differ in intensity is not considered in this review, because too few data are available (see Helversen *et al.* 2015 for data and a discussion).

Spectral properties of male songs.—The songs of most male phaneropterines consist of heavily damped impulses, which result from the contact of one tooth of the stridulatory file with the plectrum (see Figs 4, 7). (The few phaneropterines with resonant songs are listed in Hemp *et al.* 2013.) So there is typically not a single dominant frequency like in crickets, but a broad band. In Tables 1 (SM1) and 2 (SM2) the frequency with the highest amplitude is given. If there was no specific information in the respective paper, we report the maximum of the spectrum if there was a clear maximum, or otherwise the mean of the band some dB below an irregular peak.

The compilation of the data shows that most phaneropterines have relatively low-frequency songs with maxima in the audio (< 20 kHz) or low ultrasound range (Fig. 3A). However, these results may be biased for several reasons. Some studies lacked equipment capable of recording ultrasound. In addition, large species, which generally have lower songs (Del Castillo & Gwynne 2009, Heller *et al.* 2010) might have been preferred for study, or species using only ultrasound were overlooked. On the other hand, even the tiny species *Himertula marmorata* (Brunner von Wattenwyl, 1891), one of the smallest long-winged phaneropterines (tegmen length 12 mm), has a relatively low (33 kHz) frequency song (Fig. 4).

The lowest-frequency song for male phaneropterines (4 kHz) is found in *Zeuneria biramosa* Sjöstedt, 1929 (Heller *et al.* 2014) and the highest frequency song, at 90 kHz (an extreme outlier), is produced by *Ectomoptera nepicauda* Ragge, 1980 (Heller & Hemp 2014). The frequency of the songs of Barbitistini is clearly higher than in typical phaneropterines (Fig. 3B). This is in accordance with the generally smaller tegmina in this flightless group, but also with

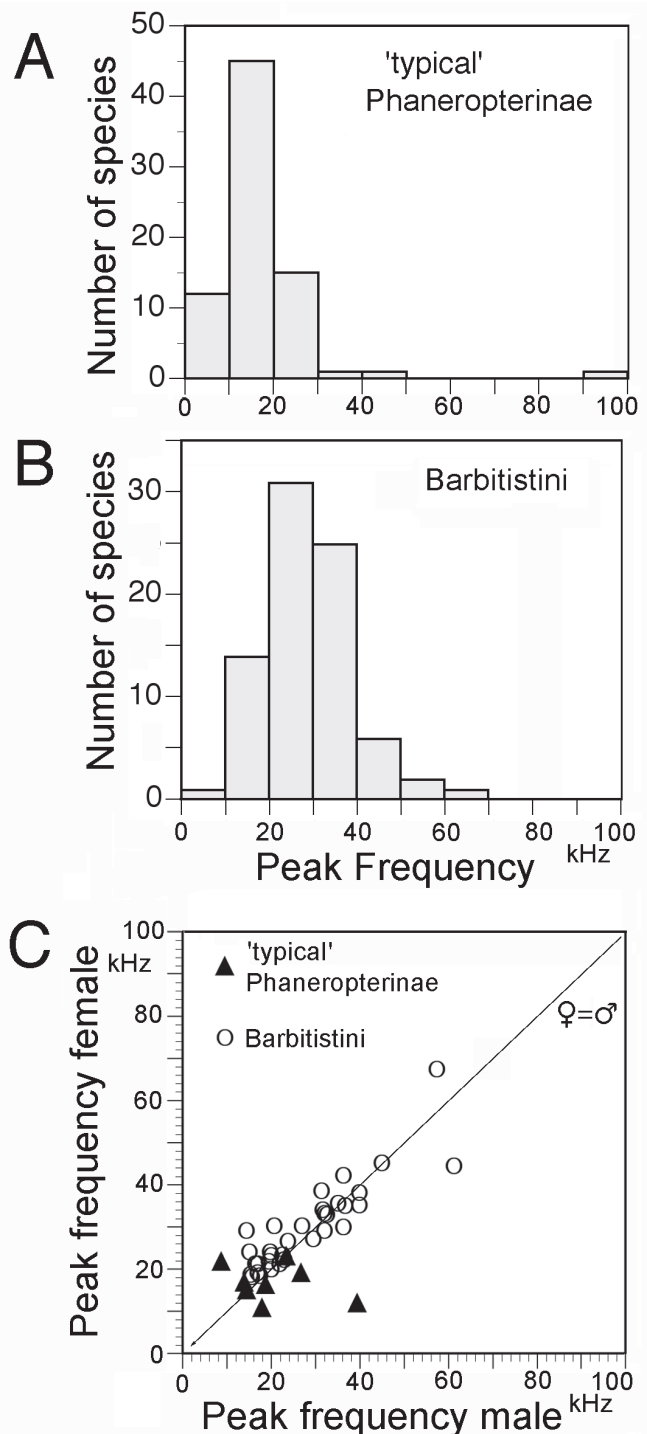


Fig. 3. Distribution of peak frequencies of male songs in typical phaneropterines (A) and Barbitistini (B) and correlation between male and female peak frequencies (C).

the requirements for the range of the signals. Given equal intensity, low-frequency signals can generally be heard over a greater distance (see *e.g.*, Heller *et al.* 2010), which may be of more importance for flying-adept, agile species than for flightless ones.

Typically, the song of tettigonioids shows more or less the same spectrum in different parts of the song, *i.e.*, there is no frequency modulation. There are, however, some exceptions. For example, the hemisyllables produced during opening and closing of the tegmina differ sometimes in spectral composition (*e.g.*, Heller &

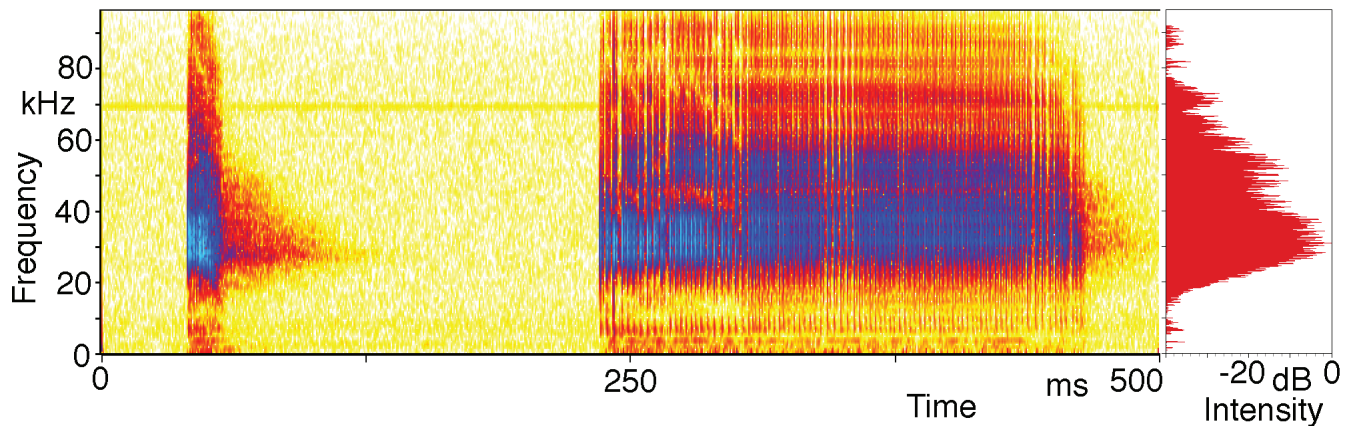


Fig. 4. Sonogram and power spectrum of male song of *Himertula marmorata*.

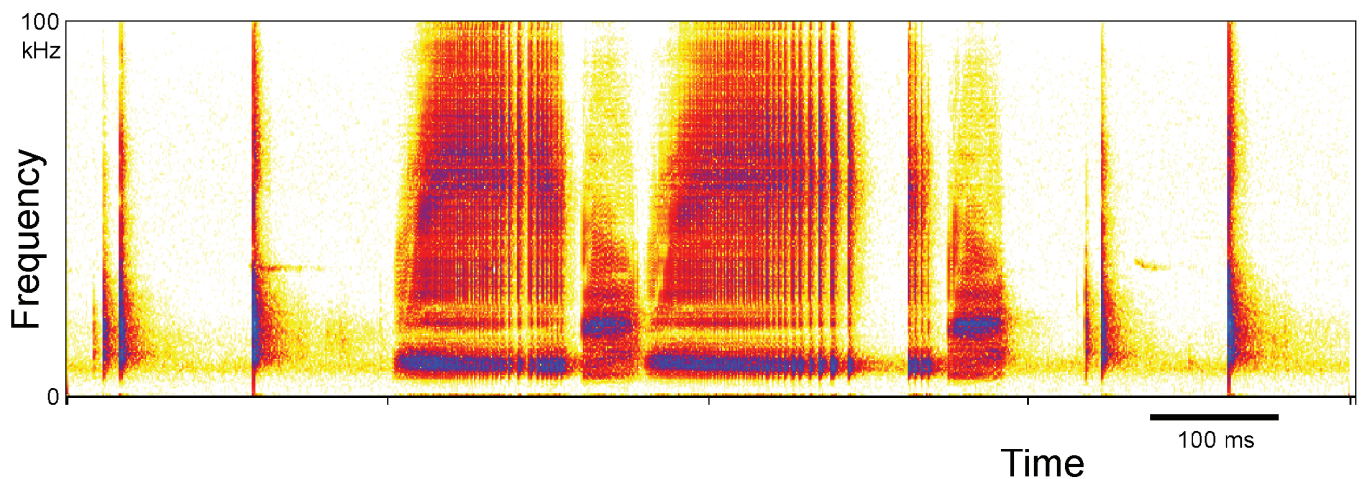


Fig. 5. Sonogram of 1-s part of male song of *Ectadia* sp. (field recording; distance microphone-animal ca. 50 cm). Details see text.

Korsunovskaya 2009). Such cases, however, are rarely documented in Phaneropterinae. One notable exception is *Poecilimon tshorochensis* Adelung, 1907, which produces narrow-banded low frequency and broad-banded ultrasound dominated song components (Heller *et al.* 2006). An even more remarkable case is found in *Ectadia* sp. (Heller & Liu, unpubl.), which has a complicated, long lasting (ca 60 s), multi-syllabic song. It starts with short, broad-banded clicks with a maximum at about 19 kHz, followed by a distinctive group of impulses paired in time with another impulse group (closing and opening hemisyllables?), and continuing in a long series. The spectra differ between the impulse groups: the first one with a peak frequency at 9 kHz, and the second at 19 kHz. During the course of the song these pairs become increasingly louder (by about 15 dB) and in the first group of impulses an ultrasound component (peak at 60 kHz) reaches in amplitude the low frequency peak (Fig. 5). A similar increase of an ultrasound component is also observed in the song of *Ectadia fulva* (unpubl.). Frequency changes have also been observed in the song of *Horatosphaga leggei* (Kirby, 1909) (Heller *et al.* 2014). Nothing is known about the function of these different frequencies nor how they are produced. Since in male-female communication, frequency differences can be evaluated by the female (see below), they may be important for males.

Spectral properties of female replies.—The spectral composition of female replies is much less known than that of males. Surprisingly, in most species, male and female spectra are quite similar, although

the morphology of the stridulatory organs is distinctly different. In Barbitistini, male and female frequencies are correlated ($r^2 = 0.78$; 33 species; Fig. 3C; unpubl. data). In the few known 'typical' phaneropterines, the same tendency can be observed, but there are outliers in both directions, female replies being higher or lower than the male song (Fig. 3C).

Temporal pattern of male songs.—In male phaneropterines, the time-amplitude patterns of the calling songs show an extremely high diversity (see *e.g.*, Figs 7, 8) so that comparisons and classifications are difficult. For a quantitative approach we have used the following three basic measurements: number of syllables within one unit of the song, number of different syllable types, and number of different pause types. While these data are largely independent of temperature, we give also the duration of one unit of the song. This is an easily recognisable character, which is, however, affected by the temperature of the singing animal.

The number of syllables per unit of the song shows a distribution strongly skewed towards the left (Fig. 6) with a mode at one in Barbitistini (more than 90 species) and in 'typical' phaneropterines (about 30 species). However, in both groups there is a long tail to the right (Fig. 6) with extremes of more than 1000 syllables per unit in Barbitistini (genus *Polysarcus*) and around 500 in 'typical' phaneropterines (genus *Tinzeda*). Concerning the duration of the song, the range in both groups is also comparable and covers four orders of magnitude, extending from less than 10 ms in *An-*

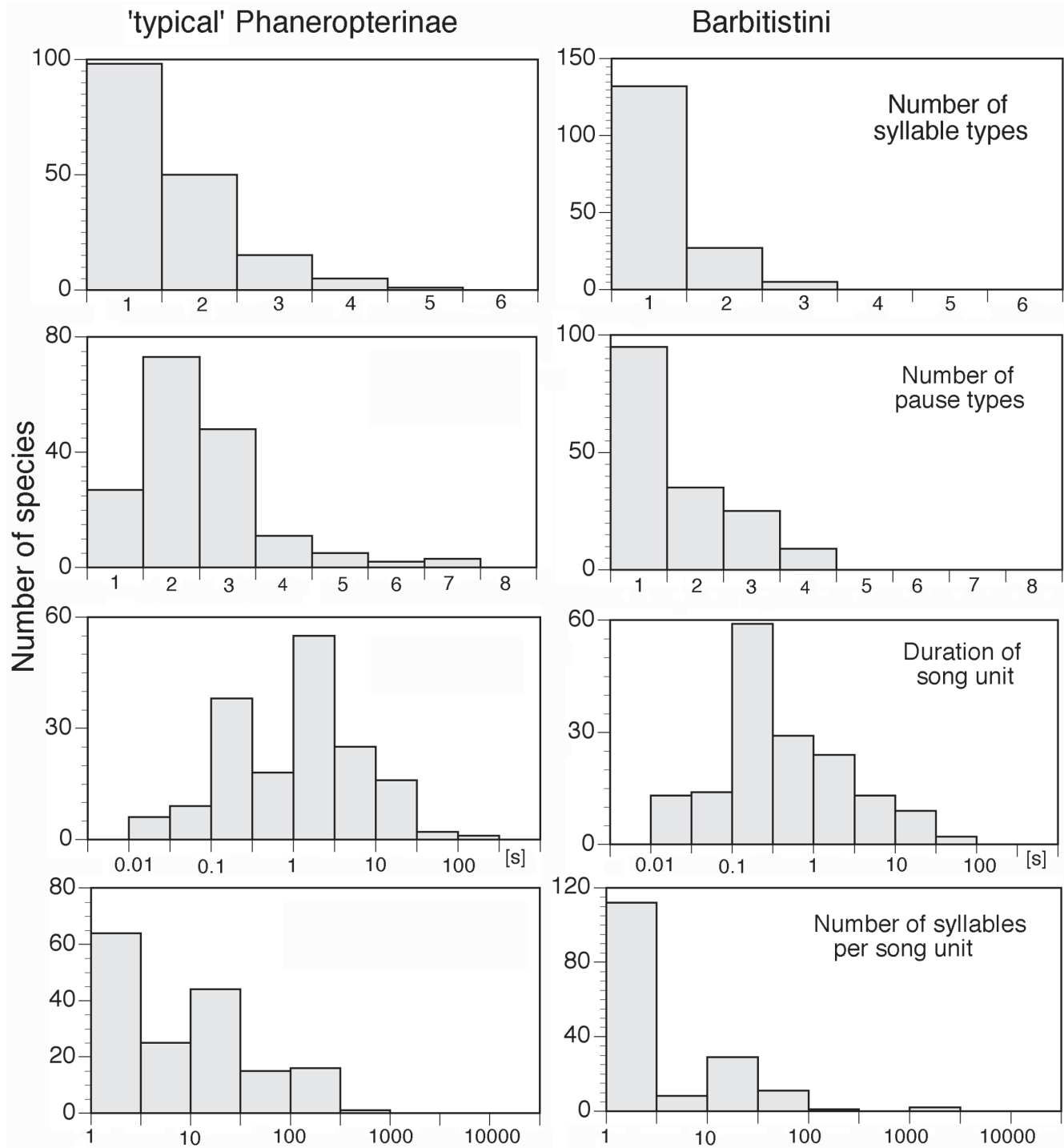


Fig. 6. Data on time pattern. Distribution of numbers of syllable types (above), numbers of pause types (second from above), duration of song (second from below) and numbers of syllables per song unit (below).

dreiniimon nuptialis to 100 s in some song forms of *Ducetia japonica* (Thunberg, 1815). Barbitistini songs tend to be shorter (median = 0.3 s) than that of 'typical' phaneropterines (median = 1 s; Fig. 6). Mode and median of the number of syllable types is one in both groups (Fig. 6), however, the mean is higher in typical phaneropterines (1.59) than in Barbitistini (1.23). Interestingly, species of the North American genus *Amblycorypha* Stål, 1873 tend to have the highest number of syllable types of all phaneropterines. These species also have the highest numbers of pause types. In general, typical phaneropterines have more different pause types ($x = 2.47$;

median = 2) than Barbitistini ($x = 1.71$; median = 1; Fig. 6). The values make it understandable that often syllable repetition rates are not sufficient to characterize songs or song differences. In species in which the same syllable is repeated several times, the rates vary between 1 and 80 Hz.

Some long-winged phaneropterine species can produce two different song types: a slow-fast song, and a long-short song (see Table SM1), but there are no data or hypotheses about their functions except for some *Phaneroptera* Serville, 1831 species, where Korsunovskaya (2008) assumes a rivalry or territorial function for

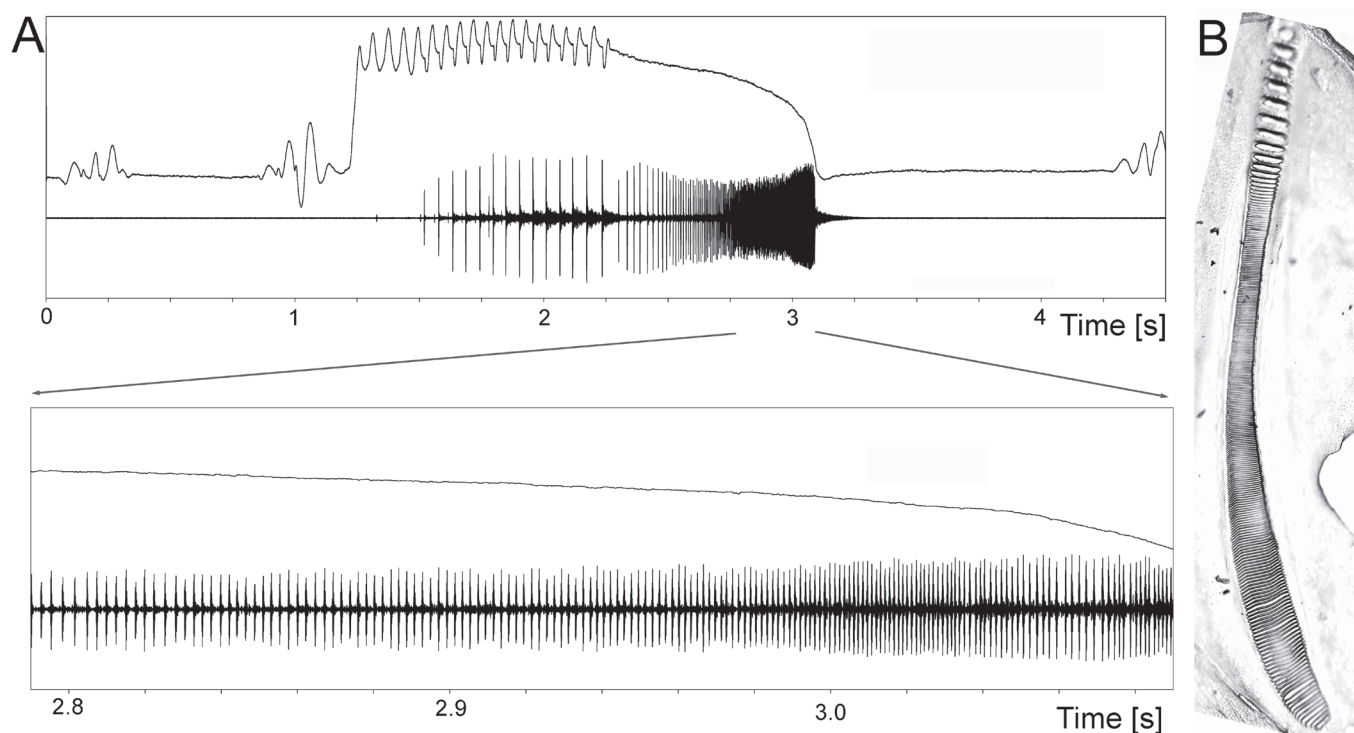


Fig. 7. *Ectadia fulva*. A) Male calling song. Oscillograms of stridulatory movement and song [synchronous registration of left tegmen movement and sound (upper line: upward deflection represents opening, downward closing; lower line: sound)]. The deflections of the movement track before and after the song result from soundless vibratory body movements. B) Stridulatory file.

the long song.

After the calling song, the males of many phaneropterine species produce – rarely, occasionally or quite often – short sound elements which resemble female replies. These sounds may even occur within the male song if the female is expected to respond at this time (e.g., Stumpner & Meyer 2001). The first hypothesis about their function as female mimicry was proposed by Stumpner & Meyer (2001). They assumed that the males might stimulate female competition. Later Bailey *et al.* (2006) and Heller *et al.* (2011) suggested that by producing these signals the males may disturb the orientation of other males towards a responding female. This idea is supported by experiments of Helversen *et al.* (2001) who showed that male *Poecilimon affinis* cannot spatially separate multiple, simultaneous female replies, and instead walk in an intermediate direction.

Production of male songs.—To produce different types of syllables, different stridulatory movements must be used. The first documented example was with *Amblycorypha uhleri* (Stål, 1876), where Walker & Dew (1972) recorded different tegminal movement patterns using high speed photography. Since then, other techniques have become available and the stridulatory movements of species in all large groups of singing Orthoptera have been recorded, including in tettigonioids (Montealegre-Z 2012), acridids (Helversen & Elsner 1977), and crickets (Robillard *et al.* 2013). However, our understanding of the production of complex songs is still very limited, including the use of irregular stridulatory files (for new movement data of phaneropterines see Iorgu 2012; Heller *et al.* 2014). Therefore we present here two remarkable examples:

1) *Ectadia fulva* Brunner von Wattenwyl, 1893. The song of this species (see also Fig. 169 in Ingrisch 1998) is produced by one complete opening and closing movement of the tegmina, but since during this time the singing male opens and closes its fore wings partly several times, the term syllable should be applied with

caution. From Fig. 7A it is evident that the male opens his wings rapidly at the beginning of the song. In the figure, before the song, two short soundless vibrations (tremulations) of the body can be recognised. With open tegmina, the male starts a series of about 20 movement cycles, during which the wings are closed only to a very limited degree. After a nearly mute beginning, during each of the small closing movements here a short, click-like sound is produced. About one second after the initial opening of the wings, the male switches to a slow closing movement which increases in speed until the end of the song. During this time many separate impulses are produced with decreasing intervals. Comparing the movement pattern with the structure of the file (Fig. 7), the male obviously stridulates first with the few large teeth at the distal part of the file and uses the long dense part of the file only during the second half of the song. The movement pattern has some similarities to that observed in species of the genus *Acrometopa* (Heller 1988), but the structure of the stridulatory file and also the song pattern are quite different.

2) *Monticolaria kilimandjarica*. The time-amplitude pattern of the complicated song of this species was described in Hemp *et al.* (2009). Similar to *E. fulva*, the teeth at the distal end of the stridulatory file are much larger than those at the proximal end of the file (see Figs 8 & 9 in Hemp *et al.* 2009). However, in contrast to most phaneropterines (and other tettigonioids), the steep side of each tooth is directed towards the wing base, indicating sound production during the opening and not the closing of the wing. This prediction was confirmed by recent movement recordings (Fig. 8). *M. kilimandjarica* seems to be the first known insect species which produces a complicated song exclusively by opening wing movements with different speed and amplitude. All other species with this type of stridulation have simple songs containing one syllable type and mostly single, isolated syllables (*Phaneroptera* spp., *Yersinella* spp., *Steropleurus* (formerly *Uromenus*) *andalusius* (Rambur, 1838)

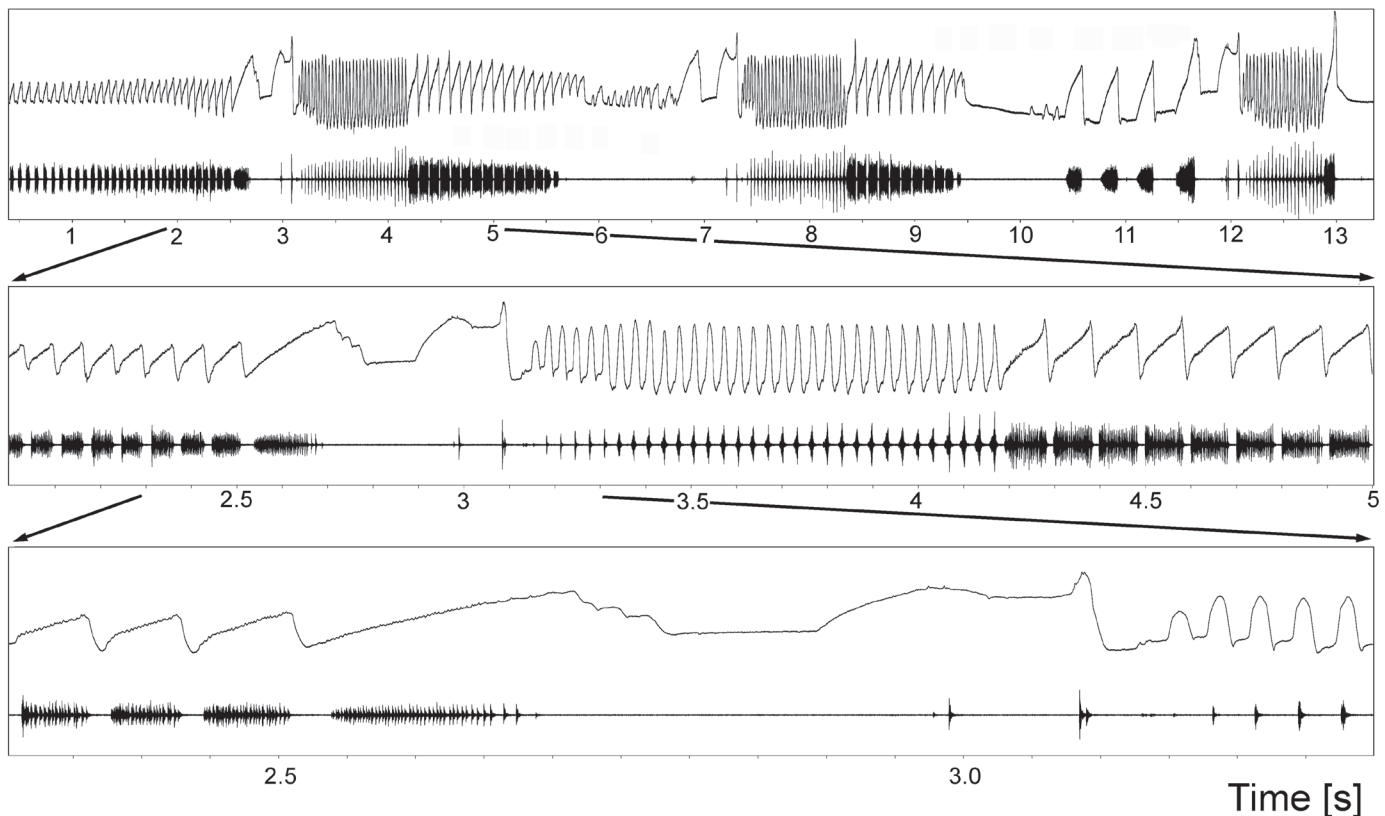


Fig. 8. Male calling song of *Monticolaria kilimandjarica*. Oscillograms of stridulatory movement and song [synchronous registration of left tegmen movement and sound (upper line: upward deflection represents opening, downward closing; lower line: sound)].

and *brunneri* (Bolivar, 1876), *Sabaterpia* (formerly *Ephippigerida*) *taeniata* (Saussure, 1898), all Heller 1988; *Ischnomela gracilis* Stål, 1873, Montealegre-Z 2012).

Temporal pattern and production of female songs.—Female acoustic signals are known from 67 phaneropterine species, including 36 Barbitistini and 31 typical phaneropterines. As recognised from the published data, they always consist of short, click-like sounds, which are typically produced by a closing movement of the wings. An example is given in Fig. 9 for *Poecilimon gracilis* (Fieber, 1853). The number of clicks is not fixed. For example, *Poecilimon laevis* (Fischer, 1853) females often produce additional clicks immediately after the initial sound producing movement (Heller & Helversen 1986). In other species females make several stridulatory movements, each one producing clicks (Villarreal & Gilbert 2013).

Hearing in males and females.—The hearing sensitivity of phaneropterines has been studied in only a few species (see SM1 and SM2). Most studies examined both sexes, but some looked at only one sex. Most results are based on neurophysiological measurements supplemented by few behavioural studies. As in many Tettigoniidae, frequency threshold curves for phaneropterines seem to be often quite broad (but see e.g., Nocke 1975, Korsunovskaya 2005) with the range of highest sensitivity typically between 10 and 20 kHz. The highest sensitivity of the receiver, and the intensity peak of the carrier frequency of the opposite sex may (e.g., *Stictophaula ocellata* Ingrisch, 1994), or may not (e.g., *Holochlora nigrotympana* Ingrisch, 1990) exactly overlap (see Heller *et al.* 1997b). However, in two Barbitistini species [*Leptophyes punctatissima* (Bosc, 1792) and *Poecilimon elegans* (Brunner von Wattenwyl, 1878)], maximum intensity of the male calling song and maximum sensitivity of fe-

male hearing are both above 30 kHz. In fact, in these two species, the most sensitive hearing range lies at the highest frequency of all phaneropterines studied so far. Interestingly, both of these small species are not very sensitive in general. In *L. punctatissima*, frequency threshold curves remain nearly flat from 10 to 60 kHz (Rössler *et al.* 1994), whereas *P. elegans* become gradually more sensitive from 10 to at least 40 kHz (Strauß *et al.* 2014). When comparing species in the genus *Poecilimon*, there is a correlation between the sensitivity of the ears (especially for ultrasound) and the size of the auditory thoracic spiracles (Stumpner & Heller 1992, Strauß *et al.* 2014).

Without going deeply into neurobiology we have to mention a hypothesis proposed by ter Hofstede and Fullard (2008) and ter Hofstede *et al.* (2010). They assume that the T-cells, which are considered to be important in many tettigonioids for sound detection of predators, are also used in male-female acoustic communication in phaneropterines.

Duetting behaviour

If two partners communicate by duetting it is useful for both if they follow certain rules, such as not to talk simultaneously – many insects are deaf during the production of their own song. Hence, the male who starts the duet must include silent gaps in his song so that he can hear a responding female. The situation can be additionally improved if the female does not answer at random, hoping to find a pause in the song, but if she can use acoustical characters (trigger; see below) in the male song predicting silent periods. On the other side, the male should not wait too long to decide if a click-like sound is a female answer to his song or an accidental noise in the environment.

The intervals between male and female acoustic signals can

be amazingly short. This is seen in *Barbitistini*, where the silent interval between the end of the male song and the female response is mostly less than 100 ms. Such short intervals are often too fast to be detected without special equipment. For example, Faber (1953: p.180) described the reactions of a female of *Polysarcus denticauda* (Charpentier, 1825) to certain parts of the male song as strictly synchronous ("streng synchron"), based on observations in the years 1929-1952. In many long-winged phaneropterine species the intervals are longer (ca 50 to 1500 ms, with the single outlier *Elimaea thaii* Ingrisch, 1998 with 3500 ms; Ingrisch 1998). Such delay times were hypothesized by Alexander (1960) as species-specific and as potentially isolating characters. This idea was supported as soon as song recordings became available (Spooner 1968, Nickle 1976). Theoretically, a female should recognize the song of a conspecific male, judge the quality of the potential mating partner, then start a timer, preferentially after a trigger, and, finally, respond at the appropriate time interval. But which songs are answered by the females, how do they time their response and what do the males do after having heard it? Two different approaches are used to answer these questions: A) computer-generated song models test and determine the essential song parameters and B) two-choice experiments using live males that differ in certain characteristics, determine which male traits, including both acoustic and non-acoustic characteristics, elicit female responses.

Concerning the first approach (A), in 1986 almost simultaneously three papers were published with similar content but on different phaneropterine species. Zhantiev & Korsunovskaya (1986) demonstrated that the duration and internal structure of the syllable was decisive for a female response, and that, depending on the species, either the beginning or the end of the syllable was used as trigger. Heller & Helversen (1986) showed that females of different species had different response delays and that the males had quite narrow response windows, outside of which they did not accept the female's answer. Lastly, Robinson *et al.* (1986), followed by Zimmermann *et al.* (1989), analysed the duetting behaviour of one species in detail and documented therewith the existence of a male response window in another species. All the above studied species had simple male songs with one type of syllable and pause. Similar results were obtained in additional phaneropterine species with some species-specific modifications (e.g., Tauber & Pener 2000, Orci 2007). Some years later, Dobler *et al.* (1994a, b) analysed a species with a complicated song and showed that the durations of syllables and pauses, including a pause before a trigger syllable, was essential to elicit the female response. In this species [*Ancistrura nigrovittata* (Brunner von Wattenwyl, 1878)] males and females even rely on the use of different carrier frequencies, a situation unique among all phaneropterine species studied so far.

Concerning the second experimental approach (B), Galliard and Shaw (1991) used two-choice tests to show that some sound parameters (e.g., intensity) were important for a male's mating success. These results were later confirmed in female phonotaxis tests (Galliard & Shaw 1992) and elaborated in two-choice preference tests with computer-generated song models on the same species (Galliard & Shaw 1996). Similar results were obtained by Tauber *et al.* (2001) using *Phaneroptera nana*. Tuckerman *et al.* (1993) tested females of *Scudderia curvicauda* (de Geer, 1773) in sequential two-choice tests. Again, females preferred those male signals that contained more sound energy (higher number of syllables). Bailey and his co-workers studied duets of some Australian species with complicated songs. In *Elephantodeta* Brunner von Wattenwyl, 1878, they discovered a male acoustic satellite behaviour whereby a second, competing satellite-male produces a very short song during

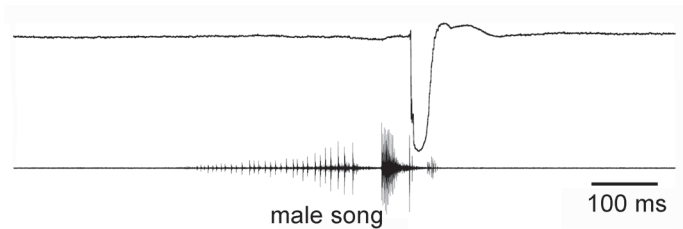


Fig. 9. Stridulatory movement of female *Poecilimon gracilis* together with male-female duet (sound). Oscillograms of stridulatory movement and song [synchronous registration of left tegmen movement and sound (upper line: upward deflection represents opening, downward closing; lower line: sound)].

an interval of the long song of the first alpha-male. Satellite-males can sometimes phonotactically attract the female, thereby stealing her from the alpha-male (Bailey & Field 2000). In a species of *Caedicia* Stål, 1874 the female answers with a variable number of clicks which may indicate her motivation (Bailey & Hammond 2004). Similar results (whereby females answered with a variable number of clicks) were also obtained by Villarreal & Gilbert (2013) in *Scudderia pistillata* Brunner von Wattenwyl, 1878, another species with a relatively complicated song.

According to experimental studies in *Barbitistini*, the triggers for releasing a female response can be placed into three groups:

1) Complete male calling song: in all of these species, the male produces a mono-syllabic calling song, and the complete song must be received for the females to respond. However, females of different species use either the beginning (*Leptophyes albovittata* (Kollar, 1833) Zhantiev & Korsunovskaya 1986; *Poecilimon ornatus* (Schmidt, 1850) Heller *et al.* 1997a) or possibly a certain duration after beginning (not excluded for *Leptophyes albovittata*) or end (*Isophya stepposa* Bey-Bienko, 1954; Zhantiev & Korsunovskaya 1986) of this syllable as trigger to set the timing of her reply. In cases where females respond to the beginning of the male song, there can be problems with song recognition, because the female has no information about the structure of that song she responds to (see Heller *et al.* 1997a).

(2) In this case, the female seems to use the pronounced syllable endings as triggers [*Poecilimon affinis* (Frivaldsky, 1867) Helversen & Wendler 2000, Helversen *et al.* 2015].

(3) In these cases, there is a trigger syllable in the male song that is 'announced' by an unusually long pause (*Ancistrura nigrovittata*; Dobler *et al.* 1994a; see also *Barbitistes* species; Stumpner & Meyer 2001). Also, syllables with unusually high amplitude may act as a trigger (*Polysarcus denticauda*: Faber 1953, Heller 1990).

Conclusions

The results of this comparison show that male calling songs in Phaneropterinae are very diverse, ranging from extremely simple to extraordinarily complex. However, on a world-wide scale, the majority of phaneropterine species with known sounds do not produce complex songs, contrary to the comments of some authors (e.g., Walker 2004, Rentz 2010). Indeed, many species have quite simple songs. However, one should keep in mind that phaneropterine acoustic communication may actually be more complicated than is currently realized, simply because intraspecific variation of song patterns is insufficiently studied and understood. Many phaneropterine species can modify their songs, and/or have special sounds when interacting and duetting. The very inconspicuous imitation

of female answers by males (see above) represents one example. Possibly some phaneropterine species with complicated male songs have integrated some female imitating sounds into the male calling song. For example, males of some species include female-like patterns in their calling songs, even when no females are present. The patterns of male phaneropterine songs appear often to be less fixed than in crickets or other tettigonioids. Another topic needing attention is the nearly unexplored possibility of change in song intensity (observed by *e.g.*, Spooner 1995). This option would be valuable to duetting species, where the singers have some information about the distance to a partner. In addition, both sexes may even switch to vibrations or use mainly the vibrational component of the song, which may make them less conspicuous to competitors and predators. Judging from the as yet low number of detailed studies of duetting species, surprising acoustic strategies may be discovered in future. Complicated songs probably evolved several times independently in the Phaneropterinae. This hypothesis is supported by the scattered occurrence of such songs on all continents, often in presumably unrelated genera. Also, some Barbitistini species with complex songs are closely related to species with simple songs (see phylogenetic tree in Ullrich *et al.* 2010). Of course, sexual selection by females choosing to respond preferentially to special song types could be an important evolutionary force driving increasing song complexity, but probably only in combination with other unknown ecological and behavioural factors.

For other important questions the data are similarly limited. What are the advantages and disadvantages of duetting? Duetting may have low costs in terms of energy and risk. For example, signal duty cycle (percentage of time spent actually sound emitting against duration of all intervals) can be low if there is no response; see Heller & Helversen 1993). For flight-adept species, a bi-directional communication might be "very efficient, because a male can search large areas for responding females by a combination of singing and flying" (Helversen *et al.* 2012). However, this hypothesis awaits field confirmation. In fact, very little is known about the mate-location behaviour of long-winged phaneropterines, and the relative costs and benefits of different strategies.

For duetting to be lost in a species (*i.e.*, evolutionary reversal to uni-directional communication), a high population density may be required, as indicated by the experiments of Helversen *et al.* (2012). Long ago, Hartley *et al.* (1974) speculated about population density as an important factor for different communication systems found in Ephemeroptera (Bradyptorinae). Population density may be also one factor (among others) determining which sex will move during the duet. There are obviously many different strategies among phaneropterines with moving or stationary males and/or females, and intermediate strategies (Zhantiev & Korsunovskaya 1986, Robinson 1990, Spooner 1995). Here not only the cost of calling in terms of energy and risk have to be considered (see Heller 1992), but also the costs and benefits obtained from multiple matings (number of offspring and increased/reduced survival by obtaining/producing a nutritious spermatophore). These questions demonstrate how deeply the acoustical communication is embedded into the mating biology of each species.

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