On the bioacoustics and morphology of some species-groups of Orthoptera

Ph.D Thesis

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1. Introduction

Orthoptera is a relatively small insect order with mostly phytophagous and mixophagous species. They have been investigated intensively for a long time mostly because of the immens agricultural damage they cause during their out breaks (e. g. Uvarov 1966, 1977; Nagy 1988, 1990; Jago 1990). Independently from economic interests they have several features which make their study interesting and important. They play a key role in the food web of grassland biocenoses and are suitable subjects for studying problems in population dinamics, community dinamics and quantitative zoocenology. It is often very informative to study Orthoptera when setting nature protection preferences. Grasshoppers and crickets are amongst the standard experimental animals of insect physiology and neurobiology. Because of their conspicuous singing behaviour (e.g. Herman 1876, Pierce 1948, Haskell 1961, Busnel 1963) they are amongst the preferred objects of ethological studies.

For successful work in the above mentioned research fields it is essential to clarify the species-level taxonomy of this group. Such taxonomic problems (see e. g. Harz 1969, 1975) have practical and theoretical reasons. Practically it is difficult to establish species and identify specimens when the traditionally used eidonomic characters show a great intra-specific and low inter-specific variation. Theoretically it is difficult to handle closely related allopatric forms (Varga 1985) because of the dimensionlessness of the biological species concept (Mayr és Ashlock 1991). Both of the above mentioned problems can often be handled examining characters that are important components of the species specific mate recognition system (Paterson 1985) of the taxa concerned.

Acoustic communication plays an important role in the pair forming behaviour of many species of *Orthoptera*. In those species acoustic signals are generally important components of their species-specific mate recognition system (see e. g. Jacobs 1953a. 1953b; Walker 1957, Perdeck 1958, Spooner 1968, Bailey and Robinson 1971, Hill et al. 1972, Zaretsky 1972, Ulagaray and Walker 1973, Paul 1976, 1977; von Helversen and von Helversen 1981, Heller and von Helversen 1986, Robinson 1990, Vedenina 1990, Vedenina and Zhantiev 1990, Doherty and Callos 1991, Stumpner and von Helversen 1992, 1994). Thus it is relevant and often highly effective to study these signals for solving taxonomic problems in morphologically uniform species-groups.

Sonotaxonomic work on Orthoptera began in the middle of the XIX cetury with the pioneering works of Yersin (1852, 1853, 1854) in Europe and Scudder (1868a, 1868b, 1893) in the USA. They used musical notes to describe the song of grasshoppers and crickets. In several cases the diagnostic value of the male calling songs was obvious even from these early works (e.g. for identifying the species of the *Glyptobothrus biguttulus*-group). Oscillographic and spectrographic analysis have become widespread in insect-bioacoustics from the ninteen-fifties (Alexander 1956, 1957b, Thomas and Alexander 1957, 1962, Walker 1962, 1963, Spooner 1968). The oscillogram-based sonotaxonomic re-examination of the European Orthoptera has begun much later, likely because the taxonomically most difficult groups live in the southern penninsulas, where orthopterologists did not used bioacoustic methods.

Until now very little bioacoustic work has been done concerning the Hungarian Orthoptera fauna (Herman 1876, Szentesi 1971). Up to now sonotaxonomic investigation have been restricted to only a few analysis (Schmidt 1990, Stumpner és von Helversen 1994) based on small samples and providing only sporadic data on our fauna. A large amount of unpublished observation and sound-recording were collocted by B. Nagy and a number of high-quality sound-recordings were collected and published by M. Országh (Országh 1982). By this work I would like to help to fill the gap of our knowledge of the

bioacoustics and taxonomy of some Hungarian or Eastern European species.

The present work is based on the oscillographic analysis of the songs of some bush-cricket and grasshopper species, which occur in Hungary, and in some cases the song and morphology of their European relatives were also studied. On the basis of their main objectives the studies included can be arranged into three groups.

– Bioacoustic and morphometric studies of some morphologically uniform species-groups in order to examine the relationships of the constituent taxa

– Some additions to our knowledge of the distribution of some species which are difficult to identify from their morphology.

– Descriptive oscillographic analysis of the songs of some species, subspecies or geographic variants, of which the songs have not been described yet.

2. Material and Methods

2.1. Bioacoustics

2.1.1. Sound-recordings studied

This work is based mainly on the sound-recordings I made during the last 4 years using specimens collected mainly from Hungary but also from Austria, Slovakia, Ukraine, Rumania and Greece. Recordings from 197 specimens of 19 species were analysed (see the appendix of the dissertation for detailed data on the circumstances of the recordings).

2.1.2. Sound-recording, analysis, play-back

Sound recordings were made using a Monacor ECM 920 and a Shure BG 4.1 condenser microphone connected to a Sony TCD-D7 DAT-recorder or to a personal computer (equipped with a Sek'D Sienna professional sound card). Sound recordings were analysed using the software Cool Edit Pro. To elicite the response song of *Poecilimon* and *Isophya* females I played back original or manipulated male calling songs from a Sony PCM-1 DAT recorder or from the

above mentioned PC through an AROWANA DC-691 or an ALTEC LANSING ACS22 speaker.

2.1.3. Bioacoustic terminology

The terminology follows Ragge and Reynolds (1998):
Pulse: a simple, undivided, transient train of sound waves (here: the highly damped sound impulse arising as the impact of one tooth of the stridulatory file)
Syllable: the song produced by one opening-closing movement cycle of the tegmina
Hemisyllable: the song produced during the opening (opening hemisyllable) or during the closing movement (closing hemisyllable) of the tegmina
Echeme: a first order assemblage of syllables
Echeme-sequence: a first order assemblage of echemes
Click: an isolated, distinct pulse
Functional unit of the song: the smallest part of the song which contains all necessary song elements and in the appropriate order to elicit female reply
Calling song: spontaneous song produced by an isolated male
Rivalry song: a special song produced by males when reacting to one another
Courtship song: a special, sometimes rhather complex song produced by a male when close to a female

2.2. Morphology

The examined specimens were collected mostly during the last 4 years. Those are conserved in 70% ethanol and stored as an attached part of the sound collection. Beside them a number of olderly collected, dried, pinned specimens were studied, which are deposited in B. Nagy's collection.

All measurements were taken using stereo microscopes (MBC-10, Studar M, Amplival) equipped with a graduated eyepiece. SEM photos were taken from dried, gold coated elytra using a Hitachi 2360N electron microscope handled by Dr. Z. Kistóf.

3. Results

3.1. Bioacoustic and morphometric studies of some morphologically uniform species-groups

3.1.1. *Euchorthippus pulvinatus* and related species in Europe

We have re-examined the taxonomy of *E. pulvinatus pulvinatus* and related western European species on the basis of morphology and song (Orci et al. 2002). We have found that *E. pulvinatus* is better treated as specifically distinct from the western European populations previously regarded as the subspecies *E. pulvinatus elegantulus* and *E. pulvinatus gallicus*; these subspecies now have to take the names *E. elegantulus elegantulus* and *E. elegantulus gallicus*, respectively. This conclusion is based on the following results. A cluster analysis suggests that *E. pulvinatus* is morphologically closer to *E. chopardi* than to *E. elegantulus*, and the calling song of *E. pulvinatus* differs from those of all the other European species of *Euchorthippus* in showing a gradual crescendo extending through most of its duration, the echemes becoming gradually longer, with more syllables and a larger number of gaps.

3.1.2. *I. modestior* and *Isophya stysi*

We studied the song and morphology of *Isophya stysi* and *I. modestior*, two closely related bush-cricket species treated as endangered in Hungary. We have found that the syllables of *I. stysi* always begin with 1-5 slowly repeated, distinct pulses, while in *I. modestior* the pulse repetition rate was evenly high throughout the whole main pulse series of the syllable. Discriminant analysis showed that on the basis of their morphology all of the examined male specimens can be classified correctly to their song-based identification, furthermore the arrangement pattern of stridulatory pegs also differed in the two species. However we were unsuccessful in finding any reliable method for identifying females from their morphology. Our results suggest that within *I. stysi* the population from the Central-Transylvanian Mountain Range differs from the other populations of this species by producing a higher number of

pulses per syllable and having more stridulatory pegs and less elongated left elytron; in these characters this population occupies an intermediate position between typical *I. stysi* and *I. modestior*. We suggest treating the two taxa as specifically distinct as they are distinguishable and the observed song differences may well be able to maintain reproductive isolation between them.

3.2. Some additions to our knowledge of the distribution of some species

3.2.1.*Ch. albomarginatus*-superspecies

I recorded and observed the courtship song and display of a number of males belonging to the *Chorthippus albomarginatus*-group (1) in the surroundings of the Hungarian side of Neusiedler See (Fertő-tó) (lake, NW Hungary), (2) in the Szigetköz (plain NW Hungary), (3) Kiskunság (plain, central Hungary), (4) Hortobágy (plain, E Hungary). I found that all the males from 2, 3, 4 produce clearly the courtship song and display which are characteristic to *Ch. oschei*, and only some of the males from 1 proved to be *Ch. albomarginatus* (Here a number of males produced irregular courtship songs and I suspect them to be hybrids of *Ch. albomarginatus* and *Ch. oschei*. The above mentioned results agree with Otto von Helversen's earlier, unpublished results [O. von Helversen pers. comm.]). These results suggest that most of the Hungarian grasshopper populations previously treated as *Ch. albomarginatus* are likely to belong to *Ch. oschei*.

3.2.2. *Isophya pyrenaea*-group

I collected some specimens belonging to the *Isophya pyrenaea* species-group (the species which were synonymized with *I. pyrenaea* by K. Harz on the basis of their similar morphology, but later turned out to be good species on the basis of their song) from the Kőszegi-hegység (mountain range, W Hungary), Aggtelek-karszt (mountain range, NE Hungary) and Zemplén-hegység (mountain range, NE Hungary). Having examined the males' calling songs and stridulatory files I found that all of them belong to *I. kraussii*. This result suggests – in accordance with the previous expectations – that the most

common member of this species-group is *I. kraussii* in Hungary. Some sonometric data measured on the songs of 15 males are presented.

3.3. Descriptive oscillographic analysis of the songs of some species, subspecies or geographic variants

3.3.1. *Isophya beybienkoi*

The male calling song and female replying song of *Isophya beybienkoi*, an endemic species of the Slovak Karst, are described for the first time and fully illustrated by oscillograms at several speeds. We have analysed the song of 7 males and 3 females collected from the type locality of the species (Orci et al. 2001). The male calling song is a long syllable-sequence composed of "A" and "B" type syllables. The arrangement scheme of these syllable-types is AAA...A - BAAA...A - BAAA...A - BAAA...A and so on (where AAA...A means a varying number of "A" syllables and "-" is a distinctively longer intersyllable interval). This complex song is highly characteristic and differs clearly from all the songs that have been described in this genus until now confirming the validity of this interesting species. Females emit a short response song with a rather variable pulse repetition pattern during the intersyllable interval immediately after the "B" syllable of the male.

3.3.2. *Isophya modesta*, with some notes on the taxonomic relationship of *I. modesta* and *I. rossica*

The male calling song and female response song of *Isophya modesta* are described and illustrated by oscillograms for the first time. We have analysed the songs of 15 males (from Hungary and Transylvania [Rumania]) and 3 females (from SW Hungary). Males emit single syllables at a rate of 0.5 - 2 / minute (20-25 ^{o}C). Each syllable consists of a main pulse-series (composed of 20-50 pulses) and a terminal pulse-series (of 10-50 pulses). The terminal pulse-series follows the main one after an interval of 4-8 seconds. Females emit their response song, a brief pulse-series with rather variable pulse-repetition pattern, after the males' terminal pulse-series (response delay: 100-220 ms) or sometimes after the main pulse-series

(response delay: 450-700 ms) or rarely after both pulse-series of the male. We have also analysed the song of some males from the Ukraine (Kanev Forest Reserve, Kiev district). That population is treated as belonging to *I. rossica* by Ukrainian orthopterologists. We have found that the oscillographic pattern of the songs of the Hungarian, Transylvanian and Ukrainian males are principally the same as that shown by the oscillogram published by Zhantiev and Dubrovin (1977) on the song of *I. rossica* from near the species type locality. On the basis of their similar calling song and morphology we think that the specific status of *I. rossica* is doubtful.

3.3.3. *Isophya brevipennis*

The male calling song and female response song of *Isophya brevipennis* is analysed and described in detail for the first time (see Otte & Naskrecki [1999] for a short sound-sample and oscillogram). I have analysed the songs of 20 males and 2 females collected from the Mecsek-hegység (mountain range, SW Hungary) and Kőszegi-hegység (mountain range, W Hungary). The male calling song is a long sequence of syllables. The syllables are composed of a main pulse-series (10-30 pulses repeated evenly) and a few after- clicks. Syllable repetition is rather regular (but varied widely between specimens: 90-160 syllables/minute at 21-24 ^{o}C). Females emitted their response song, a short pulse-series, during the intersyllable intervals of the male song. (Its delay from the end of the preceding male syllable varied between 151 and 218 ms.) The male calling song can be easily distinguished from those of all the other *Isophya* species occurring in Hungary, and using the results obtained for *I. beybienkoi*, *I. modesta*, *I. stysi* and *I. modestior* I give an identification key which uses purely song features. I selected song characters that are examinable by using a stop watch and the observer's unaided ears.

3.3.4. *Poecilimon fussi*

The male calling song and female response song of *Poecilimon fussi*, an Eastern European bush-cricket species, is described for the first time. The songs of 18 males (9 from Transylvania [Rumania] and 9 from Hungary) and 1 female (from Transylvania) have been

analysed. The male calling song of *P. fussi* is a long syllable-sequence in which the syllables follow each other in quick succession. During the whole song two types of syllable can be observed. Type "A" is a single pulse-series lasting for 150-220 ms at 22-23 ^{o} C, composed of 20-40 pulses without any after-click. In "B" type syllables a main pulse series of 120-150 ms duration (22-23 ^{o} C), containing 50-70 pulses is followed by a single (or a few) after-click(s). In the course of the whole song a cyclic alternation of two phases can be observed. Phase 1 is composed solely of "A" type syllables while phase 2 comprises exclusively "B" type syllables. The transition between the consecutive phases is quite sudden: there are only a few syllables showing transitional characteristics. Although the pulse repetition patterns of "A" and "B" type syllables are not unusual in this genus, this kind of two-phased song is unique amongst the *Poecilimon* species of which the song have been described until now. The basic unit of the female response song is composed of three pulse-groups (X, Y, Z) and is emitted while the male is producing phase 2. The first and second pulse-group is emitted during the consecutive "B-B" inter syllable intervals and the third overlaps with the second "B" syllable of the male.

3.3.5. *Pholidoptera transsylvanica*

The song of *Pholidoptera transsylvanica*, a (sub-) endemic bush-cricket of the Carpathian Basin, is described for the first time. The songs of 9 specimens from Hungary and Transylvania [Rumania] have been analysed. The stridulatory file was 3.9-4.3 mm long and contained 106-121 stridulatory pegs. Oscillographic analysis showed that the song is composed of regularly or sporadically repeated trisyllabic echemes. The duration of the echemes was temperature dependent ($r = - 0.9881$, $p<0.001$) $D = - 13.39 * T + 456.69$ [where D is the duration of echeme in ms and T is the ambient air temperature in ^{o}C between 21 and 28 ^{o}C]. Echeme repetition rate varied widely (23-133 echemes per minute at 26-28 ^{o}C). Taking into consideration the above detailed information, the songs of *Pholidoptera* species occurring in the Carpathian Basin can be classified into three groups. In the first group, which includes the song of *Ph. littoralis* and *Ph.*

frivaldskyi, the echemes are composed of more than 10 syllables (up to 50-60 syllables). In the second group, containing the song of *Ph. transsylvanica*, *Ph. fallax* and *Ph. griseoaptera*, the echemes consist of 2-5 syllables and are repeated as single echemes. In the third group echemes are repeated quickly, forming echeme-sequences of characteristic duration; the only species in the Carpathian Basin in which song belongs to this group is *Pholidoptera aptera*. In contrast with the similarity of their songs, the morphology of *Ph. transsylvanica* differs conspicuously from *Ph. fallax* and *Ph. griseoaptera*, and is much more similar to *Ph. aptera.*

3.3.6. *Pholidoptera littoralis*

We have recorded and analysed the song of some specimens of *Pholidoptera littoralis* from the Körös-Maros köz (plain SE Hungary and from the surroundings of Brasso (Transylvania) (Nagy et al. 1999). We have not found any taxonomically significant difference between their songs and the song of the Istrian (Heller 1988) and Austrian or Italian (Ragge and Reynolds 1998) populations.

3.3.7. *Stenobothrus fischeri*

We have analysed the songs of some males of *Stenobothrus fischeri* from central Hungary (Dabas) and from central (Kalambaka) and southern (Taygetos) Greece (Orci & von Helversen 2001). Our results show that the male calling songs are principally the same in Hungarian and Greek males, but their courtship songs differ conspicuously. In both regions the courtship song consists of two parts, but in Hungarian specimens during part I. a cyclic alternation of two phases can be observed as opposed to the Greek specimens where part I. contains only phase 1. The lack of phase 2 during part I makes the rate of alternation between part I. and II. in Greek specimens comparable to the alternation rate of phase 1. and 2. in the courtship song of Hungarian specimens. At present the taxonomic value of this difference is not clear; nevertheless it indicates that the Hungarian and Greek populations diverged from each other in a component of their mate recognition system, this might be enough to maintain reproductive isolation between them.