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SONG PRODUCTION AND SONG RECOGNITION IN A GROUP OF SIBLING GRASSHOPPER SPECIES (CHORTHIPPUS DORSATUS, CH. DICHROUS AND CH. LORATUS: ORTHOPTERA, ACRIDIDAE)

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SONG PRODUCTION AND SONG RECOGNITION IN A GROUP OF SIBLING GRASSHOPPER SPECIES (*CHORTHIPPUS DORSATUS, CH. DICHROUS* AND *CH. LORATUS*: ORTHOPTERA, ACRIDIDAE)

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ABSTRACT

1. *Chorthippus dorsatus*, *Ch. dichrous* and *Ch. loratus* are closely related, sympatric grasshopper species (subfam. Gomphocerinae) with few morphological differences.
2. Songs of males contain two elements: pulsed syllables produced during synchronous movements of the hindlegs (part A) and ongoing noise produced during alternating movements of the hindlegs (part B). Part A predominates in songs of *Ch. loratus* and part B in songs of *Ch. dichrous*. In *Ch. dorsatus* both parts contribute nearly equally to the songs.
3. *Ch. dichrous* and *Ch. loratus* are Eastern species, while *Ch. dorsatus* occurs all over Europe including Spain and Italy. The songs of different populations of *Ch. dorsatus* in Europe are compared.
4. Female stridulation of the three species is similar to male stridulation.
5. Females prefer—expressed by their response songs—the conspecific signals over heterospecific ones. Discrimination, however, is not perfect.
6. Tested with artificial song models, females of the different species differ clearly in their response functions for element numbers in part A, while *Ch. dorsatus* and *Ch. dichrous* females show nearly identical responses to varied durations of part B. Individuals of a Greek population with male song characteristics intermediate between *Ch. dorsatus* and *Ch. dichrous* show intermediate female response functions as well.

INTRODUCTION

Among gomphocerine grasshoppers evolutionary radiation has brought about groups of closely related species with few morphological differences (e.g. Harz 1975). The song is the most important premating isolating mechanism in many of these grasshoppers (Perdeck 1951, von Helversen and von Helversen 1975). Therefore, the bioacoustic behaviour of males and females has become a useful, if not essential, tool for taxonomic separation of morphologically similar spe-

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cies (e.g. *Chorthippus parallelus*-group and *Ch. biguttulus*-group, Faber 1957, 1960, von Helversen 1979; *Ch. albomarginatus*-group, von Helversen 1986; *Dociostaurus*, Blondheim 1990).

After considerable confusion in older literature, the group of *Chorthippus dorsatus* and related species has been revised by Maran (1953). Maran clarified the synonyms and distinguished three species: *Ch. dorsatus* (Zetterstedt 1821), *Ch. dichrous* (Eversmann 1859), and *Ch. loratus* (Fischer de Waldheim 1846), synonymous: *Ch. brauneri*, Znojko 1928. Harz (1975) followed this revision in nomenclature as does this paper.

Songs of males of the *Ch. dorsatus* group are of special interest, since they consist of two different elements (Stumpner and von Helversen 1992). While the song of *Ch. dorsatus* males has been thoroughly investigated (Faber 1929, 1953, Jacobs 1953), the song of *Ch. dichrous* males was described for the first time by Komarova and Dubrovin (1973), and later by Schmidt and Schach (1978) and Schmidt (1987). To the best of our knowledge, no publication on the song of *Ch. loratus* exists to date.

In addition to comparatively describing male and female stridulation in the three species, the following questions are addressed: Are there species-specific differences in male stridulation? Do songs of these species differ in different locations of Europe? Are females of the three species able to discriminate conspecific from heterospecific songs? Do female response functions differ for gradual variations of the two song elements?

MATERIALS AND METHODS

Animals

The animals used in this study were individuals caught in the field between 1974 and 1990. Some males and all females from *Ch. dichrous* and *Ch. loratus* which were tested in behavioural experiments were reared in captivity, indicated as F1- or F2-generation. Locations in detail are:

Ch. dorsatus (Zetterstedt 1821):
Spain: Sierra de Albarracin 1977, Sierra de Segura 1980;
Germany: Gundelfingen 1977 (Baden-Württemberg); Unterzaunsbach 1983, Leutenbach 1984, Wackersdorf 1984 (Bayern);
Austria: Alpach 1977 (Tirol);
Italy: Lajen 1984 (Südtirol); Mt. Sibillini 1989 (Marche); Mt. Gargano 1989 (*Ch. dorsatus garganicus* La Greca 1962 = *Ch. xerophilus* Schmidt 1967);

Hungary: Dabas 1990;
Romania: Miercurea Ciuc 1990;
Macedonia: Kicevo 1981, Titov Veles 1984 (wild and F1), Pletvar Pass 1984;
Greece: Mainland: Mt. Oiti 1981, Mt. Vernon 1984, Kastoria 1984, Lake Cheimaditis 1984 (wild and F1), Mt. Grammos 1984; Peleponnese; Karkalou 1989, Kalavrita 1989;
Turkey: Bozüyük, Prov. Bilecik 1983, Yeniçaga Gölü, Prov. Bolu 1986.

Ch. dichrous (Eversmann 1859):
Italy: Sabaudia (F2) 1984;
Greece: Evros-Delta 1980 (wild and F1);
Turkey: Bozüyük, Prov. Bilecik 1983, Sarikamis 1983, Boz Dagh 1986, Aladagh, Prov. Konya (1986), Burdur 1986.

Ch. loratus (Fischer de Waldheim 1846):
Macedonia: Skopje 1981, Titov Veles 1984 (wild and F1);
Greece: Strymon-delta 1977, Porto Lagos 1986;
Turkey: Kizilirmak-delta 1983 (wild and F1), Çoruh valley 1983,
Ukraine: Krym-peninsula 1990.

Identification of the species was achieved by means of the following characters: 1) In the forewing, the relative length of the apical portion and the venation (radius and media) distinguish *Ch. dorsatus* from the other two species (e.g. Maran 1953, Bej-Bienko 1964, Harz 1975, Kriegbaum, Stumpner, von Helversen, unpublished); 2) Shape of the female ovipositors distinguishes *Ch. dorsatus* from the other two species (Kriegbaum, Stumpner, von Helversen, unpublished); 3) Shape and coloration of the pronotum distinguish *Ch. loratus* from the other two species (e.g. Maran 1953, Harz 1975, own observations); 4) Shape of the male cerci distinguishes *Ch. loratus* from the other two species (e.g. Maran 1953, Bej-Bienko 1964).

Stridulation

The movements of the hindlegs during stridulation were recorded with a photoelectronic camera (von Helversen and Elsner 1978). Simultaneously, the songs were recorded with a 1/2" condensor microphone (Bruel&Kjaer) and a measuring amplifier (Bruel&Kjaer type 2606). The temperature ranged between 25 and 34°C. The signals were recorded, stored on tape (RACAL 4DS) and visualized for evaluation using a storage oscilloscope (Gould), an ink-jet-writer (Siemens Oscillomink), or a digitizing interface (DT 2128 with Stemmer Turbolab). The numbers of the two elements in each song were counted, and for single songs the cycle durations and relative phase lags of the movements between the two legs were determined.

Behavioural experiments with females

Females were kept in 7 litre or 90 litre cages under a 14/10 h light/dark cycle. Fresh grass was supplied daily. Only virgin females which were one week after the final moult or older were tested.

The ability of females to discriminate between songs was examined in two sets of experiments. In the first set, female answers were determined in response to natural songs of males or while sound recordings of natural songs or models of natural songs were played back. During these tests the temperature was around 25 to 30°C. For gradual variation of parameters, artificial song models were used. These models comprised 6 pulses of 5 ms duration and 10 ms intervals in the 'A-syllables' and ongoing sound (white noise, 1–40 kHz) in part B. The A-syllables were separated by 90 ms pauses; between the last A-syllable and part B was a 20 ms pause. See also oscillograms of the models in Figures 10b and 11b. The various song models of a test series were presented in a pseudorandom order and the female's responses were recorded by a computer (Data General Nova 2, Nova 4X). Each stimulus was presented three times in sequence and the responses to all three together were evaluated as a yes/no decision. Only those data were used in which the females responded to at least one of the stimulus-types in a program with more than 20 percent of the maximum possible number of responses. The graphs in Figures 9, 10 and 11 give the actual percentage of answered stimuli from all females. Thereby, the readiness to respond of the females of the three species can be directly compared. For more details see Stumpner and von Helversen (1992) and von Helversen (1979). The artificial stimuli were modelled on recordings of natural songs. The principal efficiency of these song models was tested with the females of all three species before test series for species discrimination started (for *Ch. dorsatus* see Stumpner and von Helversen 1992). In the experiments presented here only two parameters were varied: the number of elements in part A while keeping part B constant and the duration of noise in part B (which corresponds to the number of leg movements in part B) while keeping part A constant. The constant parameter was set to a value (syllable number for A, duration for B) effective for the respective species, and therefore differed between the species. Control experiments, however, had shown that the relative response function for one parameter was largely independent from the second parameter, while mainly the overall responsiveness was affected. During these tests with synthetic stimuli the temperature was 30°C.

Hybridization experiments

Males of one species and virgin females of another were put together in small cages for some days or for weeks. Reversed pairs were always in close proximity so that females could always hear songs of conspecific males as well.

The following combinations were made (1–3 females and 1–3 males put together): *Ch. dorsatus* females (Mt. Vernon, Greece) with *Ch. loratus* males (Titov Veles, Macedonia) and *Ch. loratus* females (Titov Veles and Pletvar pass, Macedonia) with *Ch. dorsatus* males (Kastoria and Mt. Grammos, N-Greece; Titov Veles, Macedonia; Unterzaunsbach, Bavaria). Further, *Ch. dorsatus* females (Bavaria, Germany) and *Ch. dichrous* males (Sabaudia, Italy; Aladagh and Burdur, Turkey) were put together and *Ch. dichrous* females (Aladagh and Burdur, Turkey) with *Ch. dorsatus* males (Bavaria, Germany).

Eggpods from all females were collected and treated as those from natural species, which can be bred without problems.

RESULTS

Songs of the males

Song elements

The male songs contain two different elements, which are brought about by different movements and different coordinations of the two

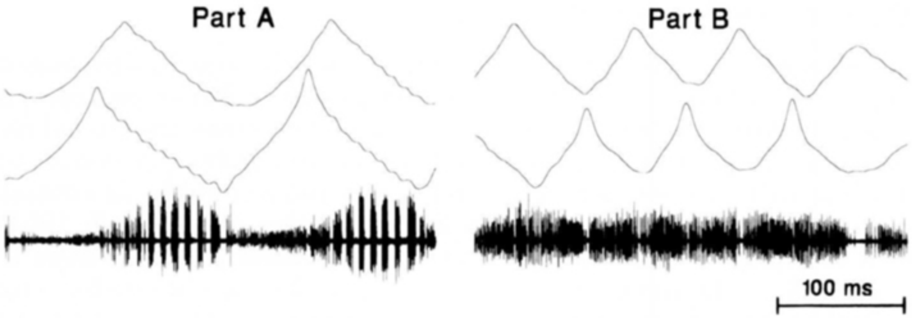

Figure 1. The traces in this figure and Figures 2 to 5 and 8 show stridulatory movements (upper two traces; up and down correspond to up and down movement) and sound produced (lower trace) during stridulation of males and females of the *Chorthippus dorsatus* group. Figure 1 gives an example from a *Ch. dorsatus* song for the two song elements in the *Ch. dorsatus group*. Part A is composed of pulsed syllables produced during synchronous stepwise down movements. Part B is composed of more or less ongoing noise produced during alternating movements.

hindlegs. Element A, a pulsed syllable, is produced during a relatively slow stepwise downward movement of the hindlegs (see Figure 1). Hereby, the hindlegs are moved with a slight phase shift, best seen in the upper reversal points (see Figure 7). The short downward movements during the stepwise downstroke, however, are exactly synchronous and thereby produce a series of short pulses. The upstroke produces a much less intense signal; thereby, the pulsed syllables are separated by pauses (or low intensity noise) of about the same duration as a syllable. One to 10 pulsed syllables (depending on the species and song types) constitute part A of a song. During part B the two hindlegs are moved in antiphase with nearly double the speed of that during part A and without interruptions in the downstrokes. In part B, both upstroke and downstroke produce an unpulsed sound. Therefore, a single "movement-element B" results in a relatively uniform noise-syllable (Figure 1) and several to many of these elements together constitute part B of a song. All three species can produce these two elements. In all songs part A precedes part B. The actual duration of each leg movement (and therefore of each song element) clearly depends on temperature (e.g. Walker 1975, von Helversen and von Helversen 1981). The number of leg movements during part A and part B, however, is little affected by temperature. Actual numbers of leg movements in part A/part B recorded at various temperatures in one individual hybrid male between *Ch. dorsatus* and *Ch. loratus* were: 20°C: 6.6/3.8, 25°C: 6.1/3.7, 30°C: 6.1/3.0, about 40°C (or higher): 6.3/1.9 (n = 10 per value). At high temperatures this male showed a tendency to reduce part B and songs became more similar to *Ch. dorsatus* courtship songs.

Relative contribution of the two elements

The clearest expression of the two elements can be seen in the song of *Ch. dorsatus* (Figures 1, 2). Four to six pulsed syllables precede an unpulsed part B of 300–400 ms duration. These values are typical for calling songs produced by spontaneously singing males (for details of the fine structure see Stumpner and von Helversen 1992). In contact with other males, they produce a louder "rivalry song" (Weih 1951) with a strongly reduced part A and an emphasized part B (Figure 2, lower right). The frequency of leg movements during the rivalry song is higher than during part B of a calling song, but the movement pattern is similar. In direct contact with females, on the other hand, they typically start to sing courtship songs of reduced intensity (Figure 2, upper right). Courtship songs are presented with much shorter intervals between single song phrases than calling songs. If a male song elicits responses in a female, a song alternation between the sexes may occur, in which males tend to sing louder than in calling songs, most obviously during part B (Figure 2, lower left).

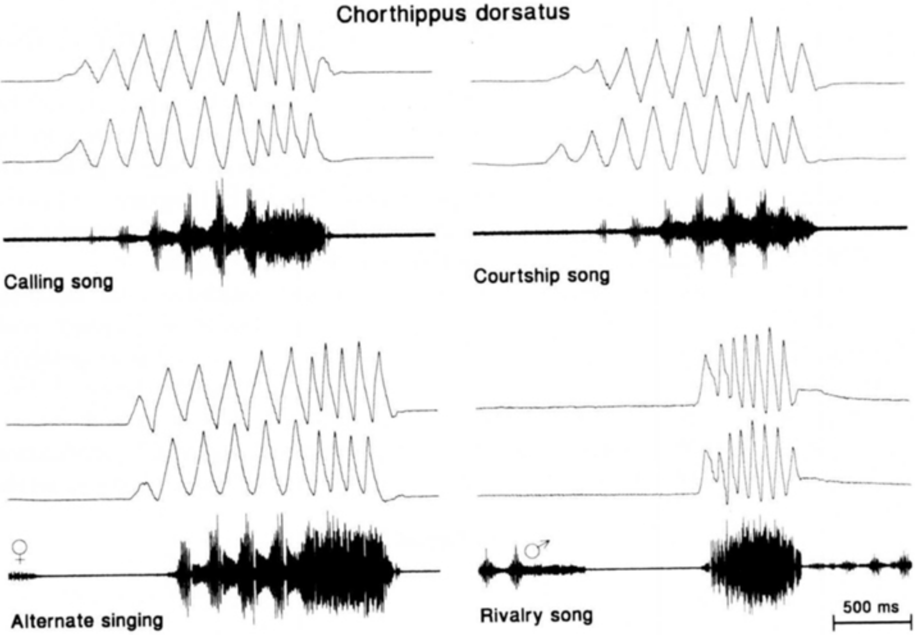

Figure 2. Male songs of *Ch. dorsatus* (all songs: Lajen, Prov. Bozen, Italy, 30°C, except rivalry song: Dabas, Hungary, 34°C). The song types differ mainly by the number of A-syllables and the duration of part B. Note the similarity of the "rivalry song" (lower right) to the song of *Ch. dichrous* (Figure 3).

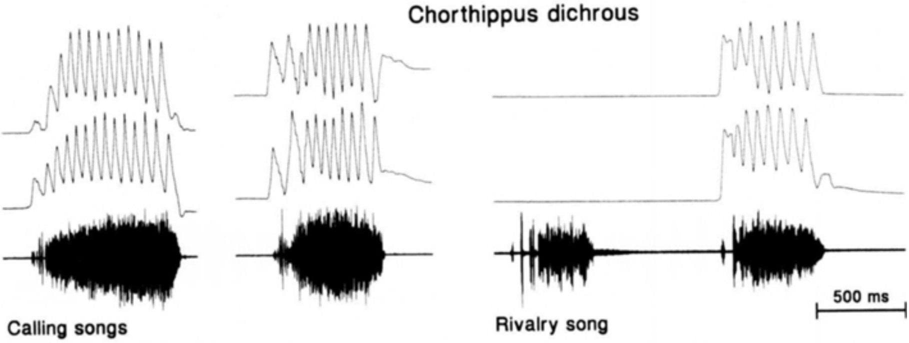

Figure 3. Male songs of *Ch. dichrous* (calling songs: Sabaudia, Italy, 31°C (left), Bozüyük, Turkey, 37°C (middle); rivalry song (Boz Dagh, Turkey, 28°C). There is not much difference between calling song, courtship song and alternate singing in *Ch. dichrous*.

Ch. dichrous songs normally start with only one, rarely with two, pulsed syllable in part A (Figure 3). This initial A-syllable, which can even be missing, is immediately followed by a long unpulsed part B lasting for about 450–800 ms (Figure 3, left). The rivalry song of *Ch. dichrous* (Figure 3, right) is nearly identical to the calling song in this species and very similar to the rivalry song of *Ch. dorsatus*.

The song of *Ch. loratus* contains many pulsed A-syllables, while part B is often not only shorter than in the other two species (up to 300 ms) but also less intense and not homogeneous (see Figure 4). Courtship songs have an even more reduced part B (Figure 4, lower left), while rivalry songs are overall shorter and leg movements resemble *Ch. dorsatus* calling songs (Figure 4, lower right).

Figure 5 gives examples of geographical variation of calling songs of *Ch. dorsatus*. The extremes are set by males from Turkey and Greece. Turkish males sing 6 to 7 A-elements, and during courtship part B may be nearly missing. In the field, males from Lake Cheimaditis in N. Greece produced spontaneous songs which were very similar to *Ch. dichrous* songs or the rivalry-song of *Ch. dorsatus* males. All of these males, however, when brought into contact with

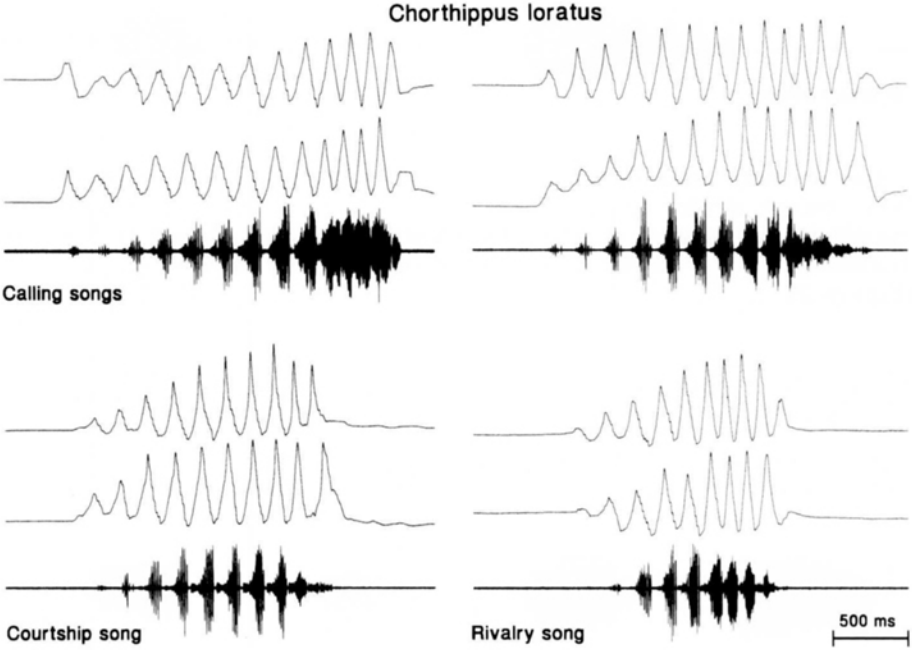

Figure 4. Male songs of *Ch. loratus* (calling songs: Porto Lagos, Greece, 29°C (left), Strymon-delta, Greece, ca. 30°C (right); courtship song: Porto Lagos, Greece, 33°C; rivalry song: Kizilirmak-delta, Turkey, 36°C). Note the gradual change (in leg movements and temporal pattern of sound) from part A to part B. Note also the gaps in part B.

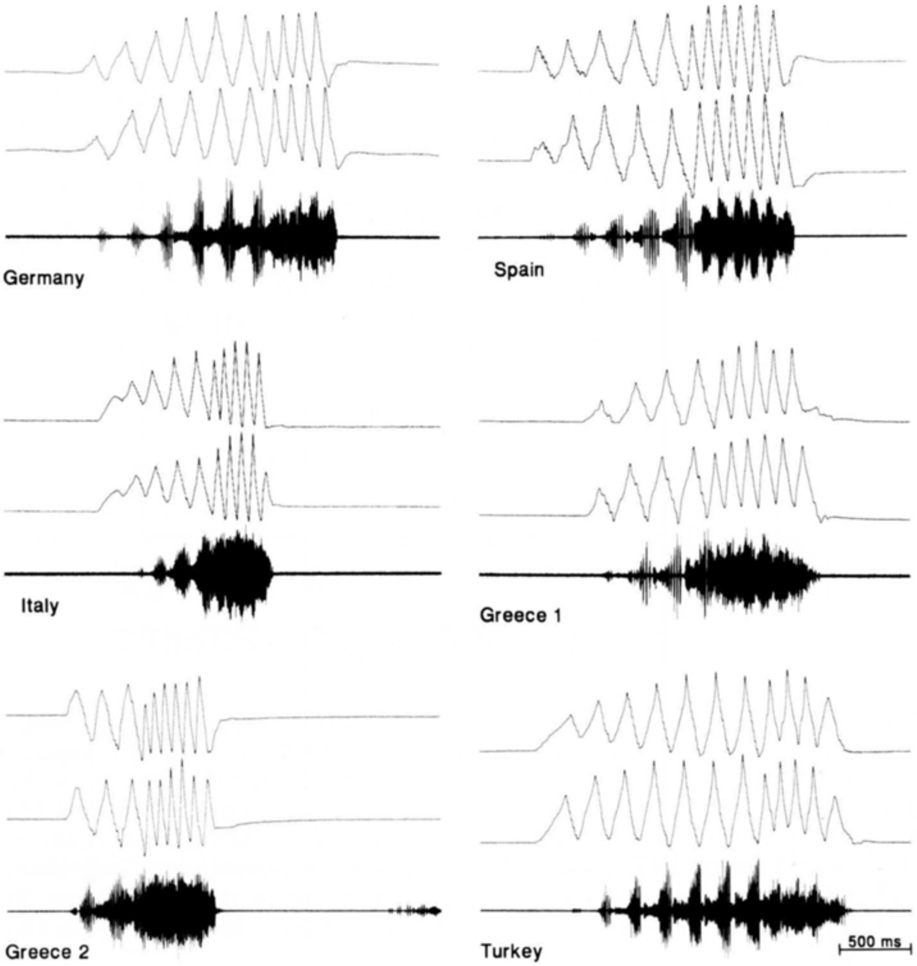

Figure 5. Male songs of *Ch. dorsatus* from different places in Europe: Germany (Wackersdorf, 30°C), Spain (Sierra de Segura, 23°C), Italy (Mt. Sibillini, 35°C), Greece 1 (Lake Cheimaditis, 29°C), Greece 2 (Peleponnese 35°C), Turkey (Yeniçaga, ca. 30°C).

females (Greece 1 in Figure 5) started to sing more similarly to normal calling songs of *Ch. dorsatus*, but the number of leg movements in part B remained unusually high. In other Greek populations (Greece 2 in Figure 5), even during courtship part A consisted of only three elements. Males from Italy, Spain and Germany produced similar songs. Animals from the Appennines (Italy) have shorter wings and have therefore been separated as a subspecies (*Ch. dorsatus garganicus* La Greca 1962 = *Ch. xerophilus* Schmidt 1967).

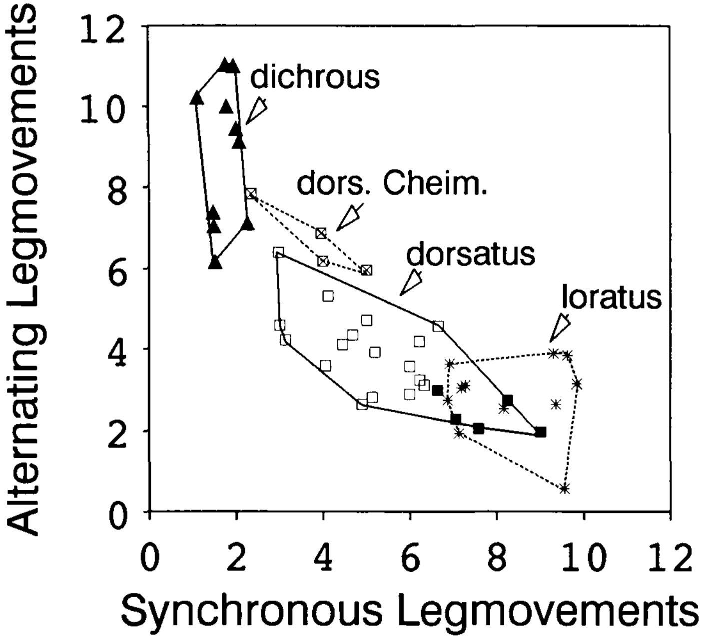

Figure 6. Number of synchronous leg movements in part A of male songs versus alternating movements in part B. Songs from the N. Greek population of *Ch. dorsatus* ("dors. Cheim." from Lake Cheimaditis) seem to be intermediate between *Ch. dorsatus* and *Ch. dichrous* songs. Songs from the Turkish populations of *Ch. dorsatus* (Bozüyük and Yeniçaga, filled squares) overlap with songs of *Ch. loratus*. Each data point represents one individual and the mean of 7 to 154 single verses. Temperatures ranged between 25 and 35 °C for *Ch. dorsatus* and *Ch. loratus* and between 25 and 31 °C for *Ch. dichrous*.

A diagram showing the correlation between the number of leg movements (corresponding to single sound elements) in the two parts of a song (calling songs and courtship songs are pooled) reveals that every species has a species-specific range of combinations (Figure 6). There is some overlap between the data of *Ch. dorsatus* and *Ch. loratus*. This overlap is caused by *Ch. dorsatus* males from two locations in Turkey (Bozüyük and Yeniçaga Gölü, black squares in Figure 6). *Ch. loratus* males of this area of overlap are from various locations in Greece and Turkey. The above-mentioned population of *Ch. dorsatus* from Lake Cheimaditis (N. Greece) lies nearest to *Ch. dichrous* and is marked by separate symbols.

Leg coordination during stridulation

When comparing the leg cycle durations and the phase relations between the two hindlegs in the three species some obvious differences can be noticed (Figure 7). All species exhibit cycle durations nearly twice as long in part A as in part B. When switching from part A to part B of a song, the drop in cycle duration in all species is accompanied by a change in the coordination of the two legs: the nearly synchronous movements change to alternating movements (Figure 7). In *Ch. dorsatus* and in *Ch. dichrous* the cycle duration and relative phase change within two (to three) leg movements when switching to element B. *Ch. loratus*, however, exhibits a slower; more gradual change within three to six leg movements (Figure 7, lower diagrams).

During calling songs, the leg movements of *Ch. dichrous* are clearly faster than those of *Ch. dorsatus* in the same temperature range (most obvious during part A in Figure 7). Moreover, the ten-

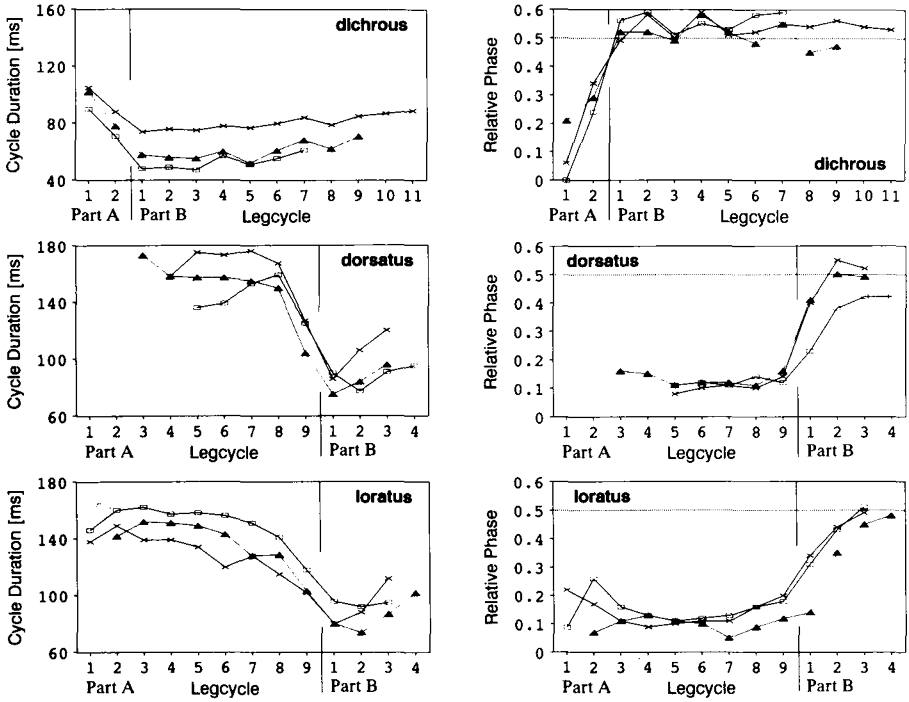

Figure 7. Leg-cycle duration (left) and phase of the "second" leg as compared to the cycle of the "first" leg starting the movement (right) for one typical song of three different individuals of the three species. A phase shift of 0 means synchronous movement, a phase shift of 0.5 (indicated by the dotted line) means alternating movement. Temperatures ranged between 32 and 34°C for *Ch. dorsatus*, between 31 and 37°C for *Ch. dichrous*, and between 29 and 32°C for *Ch. loratus*.

dency to decrease speed of leg movements during part B is much stronger expressed in *Ch. dorsatus* and *Ch. loratus* than in *Ch. dichrous* (Figure 7). Interestingly, *Ch. dorsatus* has a higher rate of leg movements during rivalry songs than during calling songs. This rate is similar to that in *Ch. dichrous* calling songs (compare Figures 2 and 3). *Ch. loratus* males may sometimes finish their songs even before the leg movements become alternating.

Songs of the females

The songs of receptive females of all three species, produced in response to male songs, show the same basic features as the male stridulatory patterns (Figure 8). Movements usually start with slow synchronous leg movements and then switch to faster ones. The songs, however, are much more variable — especially during part B — and show more gaps and pauses and are less intense. Females often insert fast up and down movements — especially during part B — (with a rate similar to the flight rhythm, see e.g. Elsner 1983). This pattern is usually the one with the loudest sound production.

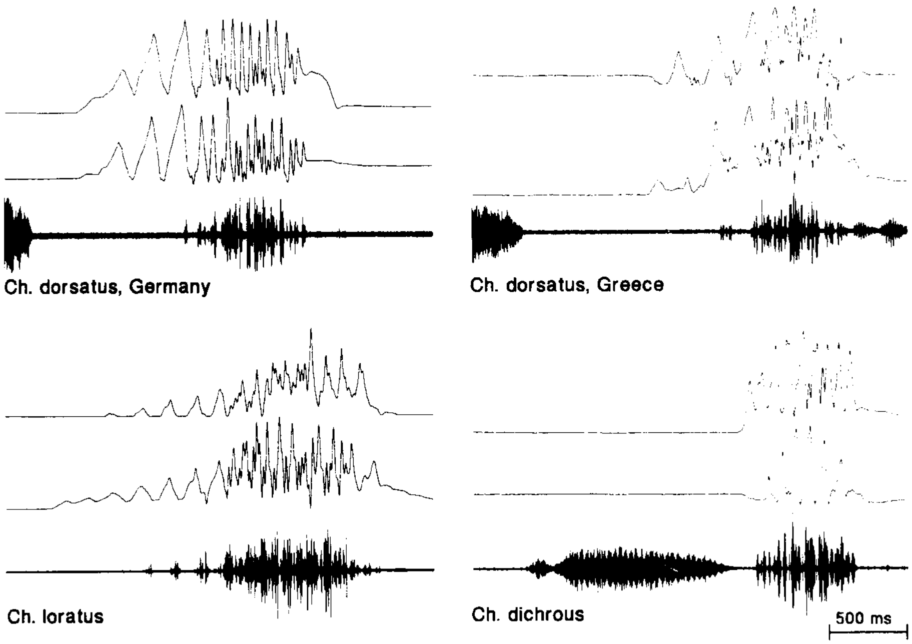

Figure 8. Songs of females of the three species in response to male calling songs (*Ch. dorsatus* Germany: Wackersdorf, ca. 30°C; Greece: Lake Cheimaditis, 31°C; *Ch. loratus*: Titov Veles, Yugoslavia, ca. 30°C; *Ch. dichrous*: Sabaudia, Italy, 30°C). Note the high frequency of some leg movements during part B-production in all females.

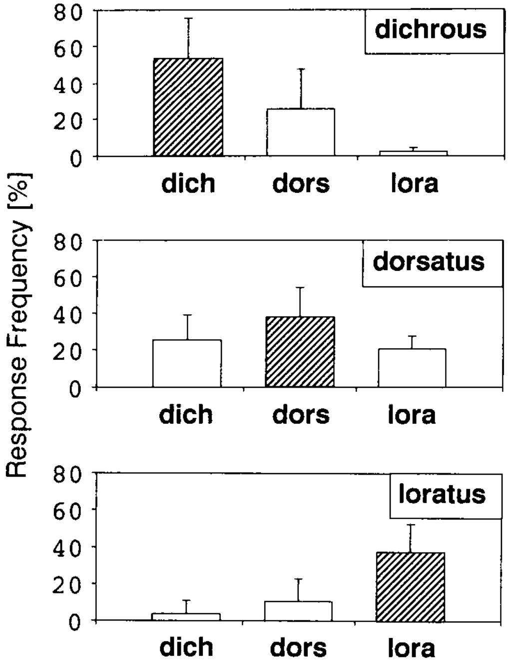

Figure 9. Female response frequencies (unnormalized, positive standard deviation of females inserted) of the three species to tape recorded natural songs (recorded at 25–30°C) or to artificial models of calling songs of all three species. The hatched columns indicate the responses to the conspecific signal, which is most effective in all three species. *Ch. loratus* females seem to be most selective. N per data point: *Ch. dichrous*, 4 females, n = 166; *Ch. dorsatus*, 6 females, n = 290; *Ch. loratus*, 4 females, n = 846. Temperature during tests: 25–30°C.

Discrimination of song patterns by the females

Figure 9 shows the response frequencies of females of the three species to tape recorded or synthesized male songs. Each species shows a clear preference for the conspecific songs (hatched bars in Figure 9); mistakes, however, occur frequently, though rarely between *Ch. dichrous* and *Ch. loratus*.

If females distinguish between songs of the different males, they seem to count the number of A-syllables and to measure duration of part B. More detailed experiments with gradual variation of these two parameters were made to test this.

Concerning the number of A-syllables, females of the three species showed species-specific response functions (Figure 10). Those of *Ch. dorsatus* and *Ch. dichrous* showed considerable overlap. The

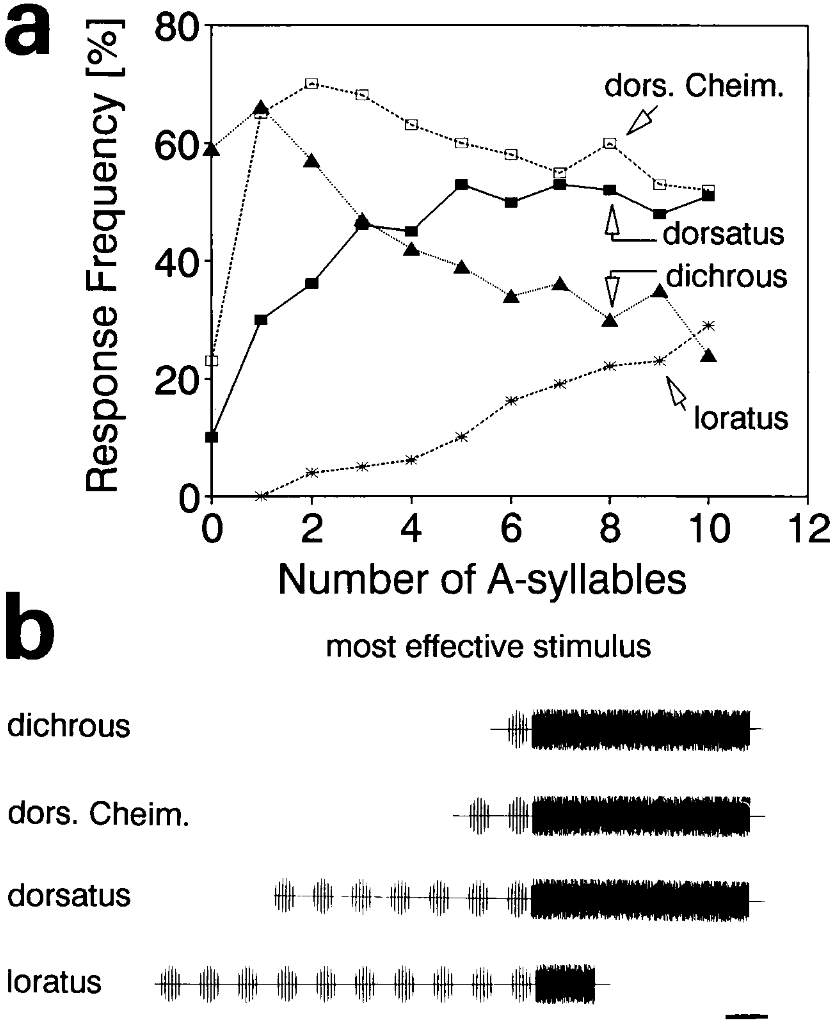

Figure 10. (a) Female response frequencies (unnormalized) to models of male songs with varied number of A-syllables (most effective stimulus for each species given in (b)). The duration of part B was kept constant, but differed between the species (1000 ms for *Ch. dichrous* and *Ch. dorsatus*, 270 ms for *Ch. loratus*, see (b)). Sample sizes and interindividual variation: *Ch. dorsatus* (filled square), 7 females (Leutenbach, Germany), n = 480 tests per data point; response maxima of the 7 individuals at 3,5,5,6,6,7 and 10 A-syllables; N.Greek population (dors. Cheim., open square), 3 females (Lake Cheimaditis F1), n = 268, response maxima at 1,3 and 9 A-syllables; *Ch. dichrous* (filled triangle), 4 females (Sabaudia F2, Italy), n = 262, response maxima at 0,1 and 2 (2x) A-syllables; *Ch. loratus* (asterisks), 3 females (Titov Veles F1, Macedonia; Kizilirmak-delta F1, Turkey), n = 177 response maxima at 9 and 10 (2x) A-syllables. Temperature during tests: 30°C. Bar in the lower right of (b): 200 ms.

females of *Ch. dichrous* preferred songs with no, one or two A-syllables, but their response probability declined only slowly with increasing numbers of A-syllables (males will never produce more than two A-syllables). Females of *Ch. dorsatus* preferred songs with more A-syllables; their response frequency was maximal with stimuli comprising more than four A-syllables. Interestingly, females of the above mentioned population from Northern Greece (dors. Cheim. in Figure 10) exhibit a response function which is nearly intermediate between *Ch. dorsatus* and *Ch. dichrous* — like the songs of their males. The females of *Ch. loratus* never responded to songs with just one A-syllable and from our data we cannot exclude that more than 10 A-syllables might be even more effective for them.

Concerning duration of part B (Figure 11), there was a striking similarity between the response curves of *Ch. dorsatus* (including the Greek population) and *Ch. dichrous*. Both species responded best to song models with 1000 or 1600 ms part B, which is longer than any male actually is singing. Again, *Ch. loratus* differed most from the other species and was most selective—strongly preferring a short part B. Songs without part B were more effective than for any of the other two species. This indicates that *Ch. loratus* females might accept songs of *Ch. parallelus* (e.g. Faber 1960), which may occur syntopically at some locations. However, we did not follow up this question in detail.

Hybridization between species

As shown above, there is a grasshopper population in N. Greece (lake Cheimaditis) which has male song characteristics and female response functions intermediate between *Ch. dorsatus* and *Ch. dichrous* (Figures 6,8,10,11). Specimens of this population are morphologically very similar to *Ch. dorsatus*. Natural hybridization may have caused these intermediate phenotypes (e.g. Ragge 1981, 1984). Therefore, we performed some hybridization experiments in the laboratory.

Long copulations were observed only between *Ch. loratus* females and *Ch. dorsatus* males, even between syntopic pairs from Macedonia. Some copulations between *Ch. dichrous* males and *Ch. dorsatus* females took place, while two observed mating attempts of *Ch. dorsatus* males with *Ch. dichrous* females remained without success —the males finished their copulation efforts after a while, although the females did not obviously object to their attempts. Offspring only hatched from one type of cross, namely *Ch. dorsatus* males and *Ch. loratus* females. Altogether 109 1st instar nymphs hatched from 51 eggpods (66 from Bavarian males, 27 from Macedonian males, 16 from a cage with both Greek and Bavarian

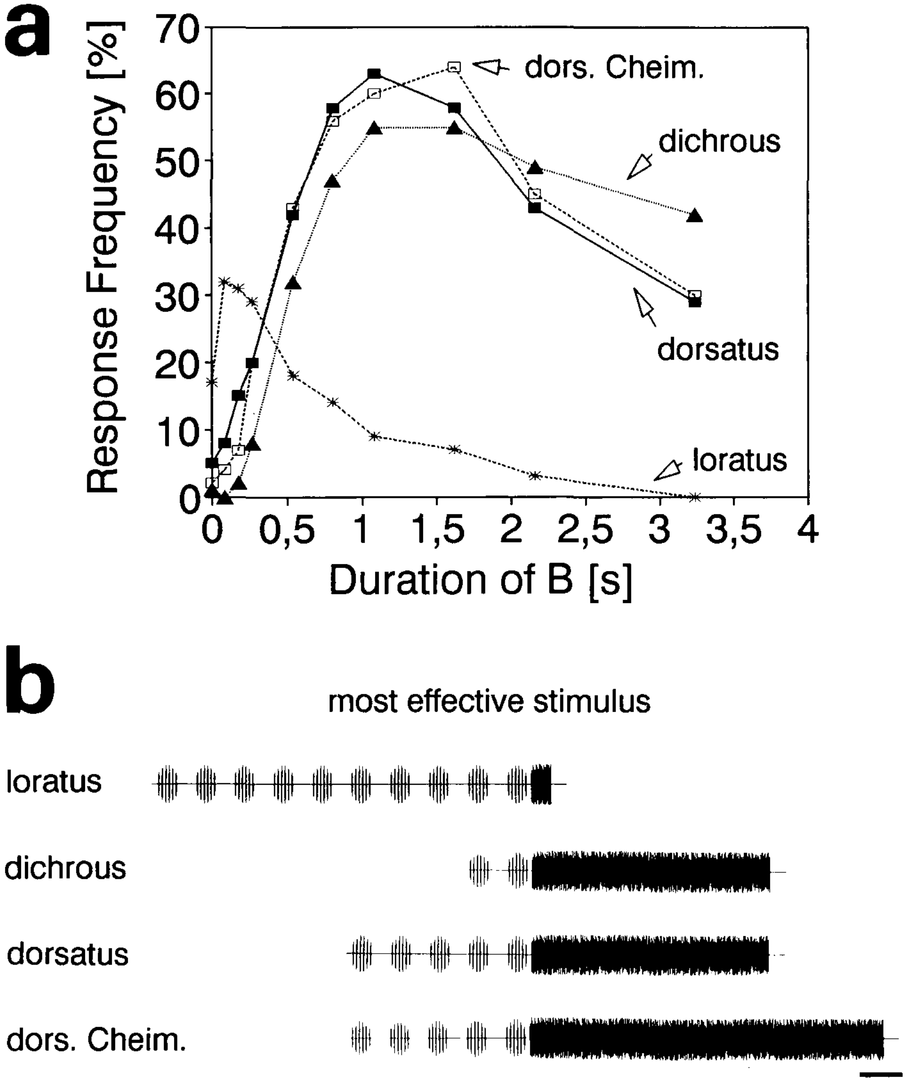

Figure 11. (a) Female response frequencies (unnormalized) to models of male songs with varied duration of part B (most effective stimulus for each species given in (b)). The number of A-syllables was kept constant but differed between the species (see (b)). Symbols as in Figure 10. *Ch. dorsatus*, 4 females (Wackersdorf, Germany), n = 329 tests per data point; response maxima of the individuals: 810 (2x) and 1620 (2x) ms part B; dors. Cheim, 2 females (Lake Cheimaditis F1, N. Greece), n = 181; response maxima: 810 and 1620 ms part B; *Ch. dichrous*, 2 females (Sabaudia F2, Italy) , n = 176; response maxima 810 and 2160 ms part B; *Ch. loratus*, 3 females (Titov Veles F1, Macedonia; Kizilirmak-delta F1, Turkey), n = 243; response maxima 90, 180 and 270 ms part B. Temperature during tests: 30°C. Bar in the lower right of (b): 200 ms.

males). Ninety-seven of the nymphs (from all three types) developed to vital adults, among them all 27 from the cross between syntopic Macedonian males and females. For more than two weeks, many adults were kept together in one cage, however, no second generation offspring could be obtained. We did not try backcrosses.

DISCUSSION

Correspondence of sender and receiver

When the relative importance of part A and part B in male calling songs is compared, there is a clear sequence in the three species: *Ch. loratus* produces a long part A but a short part B; in songs of *Ch. dorsatus* both parts are well expressed, while *Ch. dichrous* exhibits songs with a very short part A and predominant part B (see Figures 2–4).

These traits find a general correspondence in the IRMs of the respective females: *Ch. loratus* females prefer long parts A, while the shortest parts B tested (90 ms) were most effective (Figures 10 and 11). This corresponds well to male songs. The highest response frequencies of *Ch. dorsatus* females are elicited with 5 to 7 A-syllables (Figure 10), as one can find in a typical male song. However, part B of 1 to 1.6 seconds is most attractive (Figure 11). Models with such a part B must be considered as a supernormal stimulus for the females, since *Ch. dorsatus* males never sing parts B lasting for longer than about 600 ms (for detailed discussion of this aspect see Stumpner and von Helversen 1992, von Helversen and von Helversen 1994). The same holds true for the response behaviour of *Ch. dichrous* females, which for part B is very similar to that of *Ch. dorsatus* (Figure 11). On the other hand, for *Ch. dichrous* females, songs with no, one or two A-syllables are most effective, closely resembling the situation found in male songs. Astonishingly, even many more A-syllables than in natural songs, reduce the response probability of *Ch. dorsatus* not at all, and of *Ch. dichrous* females only by 50 percent (Figure 10). Therefore, the selection pressure against avoiding songs with more than normal A-elements does not seem to be especially high in either species—although this trait differs sufficiently to serve as a criterion for species discrimination (see Figure 9).

Acoustic communication as species isolating mechanism?

Female response functions (Figures 10,11) reveal considerable overlap of response probabilities between species. This indicates that the acoustic communication cannot suffice for ensuring species isolation. Females of *Ch. loratus* indeed discriminate the songs of *Ch. dichrous* effectively and vice versa. However, both species respond to songs of *Ch. dorsatus*, although with a lower probability than to conspecific songs (Figure 9). For *Ch. dichrous* the additional problem arises that conspecific song and rivalry song of *Ch. dorsatus* are virtually indistinguishable. However, it is just the pairs *Ch. dichrous* and *Ch. dorsatus* and *Ch. dorsatus* and *Ch. loratus*, which occur at least in some places within hearing range.

The incomplete acoustic isolation leads us to the conclusion that there must be other important factors for isolation of these species. Possibly, different spectra of pheromones might play the key role as premating isolating mechanisms (compare effect of removal of antennae in *Ch. parallelus*, Ritchie 1990). During the hybridization experiments we often noticed an obvious ignorance of females by heterospecific males (in contrast to earlier observations with hybridizations in the *Ch. biguttulus* group, von Helversen and von Helversen 1975; in this group acoustic communication seems to be the main isolating factor, see also Perdeck 1957; nevertheless, natural hybrids seem to occur, Ragge 1981, 1984; own observations). In addition, there seem to be postmating isolation mechanisms, as the failure to interbreed *Ch. dichrous* and *Ch. dorsatus* or to breed an F2-generation of *Ch. loratus* x *dorsatus* indicate (cf. also Hewitt et al. 1987, Virdee and Hewitt 1992).

Distributional and ecological overlap

Since the three species have a large area of sympatric occurrence (from SE. Europe and Anatolia into Asia) there can be no doubt about their species status (Maran 1953). Despite some differences in ecology, their habitat requirements obviously are so similar that syntopic occurrences are not rare. *Ch. dichrous* is mainly distributed in grasslands with long, hard prairie grasses. *Ch. loratus* lives, at least partially, on very dry grass covered slopes, sometimes close to bushes or trees. *Ch. dorsatus*, in Mid-Europe, prefers wet meadows, but in the Alps it also occurs in dry valleys. In the Appennines this species lives on extremely dry, stony hills. Harz (1975) synonymized the short-winged *Ch. "xerophilus"* Schmidt 1967 with *Ch. dorsatus garganicus* La Greca 1962. This subspecies stridulates like the nominate form (Figure 5). Syntopic occurrences of *Ch. dorsatus* and *Ch. dichrous* are usually found in wet areas with high grasses, e.g. in the Hungarian Puszta (Nagy 1983 (sub *Ch. loratus*)) or at the "Neusiedler See" (Schmidt and Schach 1978); we found them syntopically in Turkey, Prov. Bilecik, near Bozüyük. *Ch. loratus* and *Ch. dorsatus* meet with highest probability on dry grasshills (personal observations at the Pletvar-pass, Macedonia). *Ch. loratus* obviously reduces temporal overlap with other species by appearance relatively late in the year usually two to several weeks later than the other two species).

Hybrid populations between *Ch. dichrous* and *Ch. dorsatus*?

A population of *Ch. dorsatus* from wet, steppe-like meadows close to the waterfront of the Lake Cheimaditis in Northern Greece showed acoustic characteristics intermediate between *Ch. dorsatus* and *Ch. dichrous*: the males produced "*dichrous*-like" songs in the field (without the typical situation of nearby rivalling males), longer parts B (Figure 6) with higher speed of movement (Figure 5). Females accepted songs with one or two A-syllables better than those with 5 or more A-syllables (Figure 10). Possibly, these animals descend from a *dorsatus*-population, which experienced an introgression of *dichrous*-genes. The biotope, wet meadows with high, hard grasses, would fit this assumption.

Other populations in Macedonia and in Greece (wet meadows at Kalavrita and Karkalou, Peloponnese; bank areas of the lake Skutari and other places) have not yet been investigated in great detail, but the data available indicate that they belong to a similar, intermediate type. On the other hand, in Greece we also found typical *Ch. dichrous* populations (e.g. in the Evros delta) and typical *Ch. dorsatus* populations (e.g. in Mt. Vernon, Smolikas and Grammos). In the laboratory, however, we failed to hybridize *Ch. dorsatus* and *Ch. dichrous* (see above).

Finally, we want to direct the attention to the songs with many A-syllables in *Ch. dorsatus* populations of Bozüyük and Yeniçaga Gölü (Turkey, Figures 5,6). These songs might be understood as a result of "character displacement" against *Ch. dichrous* (syntopic in Bozüyük). Alternatively, we cannot exclude an introgression of *loratus*-genes.

Phylogenetic relationships

The calling songs of the three closely related species *Ch. dorsatus*, *Ch. dichrous* and *Ch. loratus* are characterized by two song elements, which are produced during different coordinations of the hindlegs. Thereby they differ from the closest relatives within the subgenus *Chorthippus* s. str., namely the *Ch. parallelus* group. Species of this group exhibit plesiomorphic songs (for the genus *Chorthippus*) produced by simple up and stepwise down movements with nearly synchronous activity of the hindlegs. These songs closely represent part A of songs in the *Ch. dorsatus* group. Independently of the calling song, *Ch. parallelus* males can also produce a rivalry song with faster alternating movements of the hindlegs corresponding to part B of songs in the *Ch. dorsatus* group. This situation is consistent with the hypothesis that the basic song pattern of the *Ch. dorsatus* group has evolved by coupling calling song to rivalry song, as they can be found today in the *Ch. parallelus* group (Faber 1929, 1932, 1960, Stumpner and von Helversen 1992). The much more complex courtship songs in the *Ch. albomarginatus* group (von Helversen 1986) exhibit alternations between slow and fast leg movements as well, and it is conceivable that these songs represent an advanced development of *Ch. dorsatus* songs (von Helversen 1986). From morphological characteristics (especially the parallel pronotal side keels) a close relationship between the *Ch. parallelus* group, *Ch. dorsatus* group, and *Ch. albomarginatus* group has been hypothesized before (e.g. Tümpel 1901, Harz 1957).

Phylogenetic relations within the *Ch. dorsatus*-group

Calling song and rivalry song of *Ch. dichrous* males are nearly identical and are very similar to rivalry songs of *Ch. dorsatus*. The number of A-syllables is strongly reduced and the legs are moved at a higher speed than during *Ch. dorsatus* calling songs. Oscilloscopic analysis of sound signals already indicated the existence of two element types also in *Ch. dichrous* songs (Komarova and Dubrovin 1973, Schmidt and Schach 1978), but only a registration of the actual leg movements reveals that nearly every *Ch. dichrous* song starts with one or two A-elements (Figure 3). Therefore, *Ch. dichrous* can be conceived as having separated as a “rivalling tribe” of *Ch. dorsatus*; and part A of its songs obviously has been secondarily reduced. The high degree of morphological similarity already signifies that *Ch. dorsatus* and *Ch. dichrous* are sister taxa.

It is more difficult to judge the evolutionary position of *Ch. loratus*. The more graded instead of sudden transition between the two movement types in a song might represent the more primitive state. A less derived underlying neuronal network generating the rhythmic motor pattern might simply need more time to switch between two opposite types of leg coordinations. However, one might also argue in the opposite way, namely that the more abrupt switch in *Ch. dorsatus* and *Ch. dichrous* expresses the origin of the signal as being composed from two parts, while in *Ch. loratus* there is a development away from this situation.

Taxonomic position of *Ch. jucundus*

There is one other grasshopper species in Europe, *Ch. jucundus*, which may more closely belong to the *Ch. dorsatus* group. This relatively large species is distributed in SW-Europe (S. France and Spain) and shows several morphological similarities to *Ch. dorsatus* and *Ch. dichrous*. Males produce a calling song comprising alternating element B-type leg movements. Possibly, *Ch. jucundus* represents an advanced development of *Ch. dichrous* in a SW-European glacial refuge with a complete reduction of part A. The taxonomic relationship of this species should be assessed in detailed morphological and biochemical investigations.

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