

# Non-Ecological Radiations in Acoustically Communicating Grasshoppers?

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We dedicate this chapter to Professor Dr. Otto von Helversen, who studied the evolution of acoustic communication in grasshoppers for more than 30 years and who tragically died during drafting this review.

**Abstract** The analysis of mechanisms of how populations differentiate and new species arise is fundamental for understanding the evolution of biological diversity. Mating preferences and sexually selected characters can rapidly diverge between populations, and this can probably lead to premating reproductive isolation and hence the evolution of new species. We have investigated the role of a complex bidirectional acoustic communication system for the radiation of grasshoppers of the subfamily Gomphocerinae. Species are characterized by species-specific songs, which result from complex stridulatory movement patterns of both hind legs. A molecular phylogeny indicates that within the genera *Chorthippus* and *Stenobothrus* several species-rich taxa diverged recently and thus represent independent radiations. Divergence in allopatry and hybridization after secondary contact are two mechanisms that led to new song types and female preferences and thus may have contributed to rapid speciation by the evolution of premating reproductive isolation.

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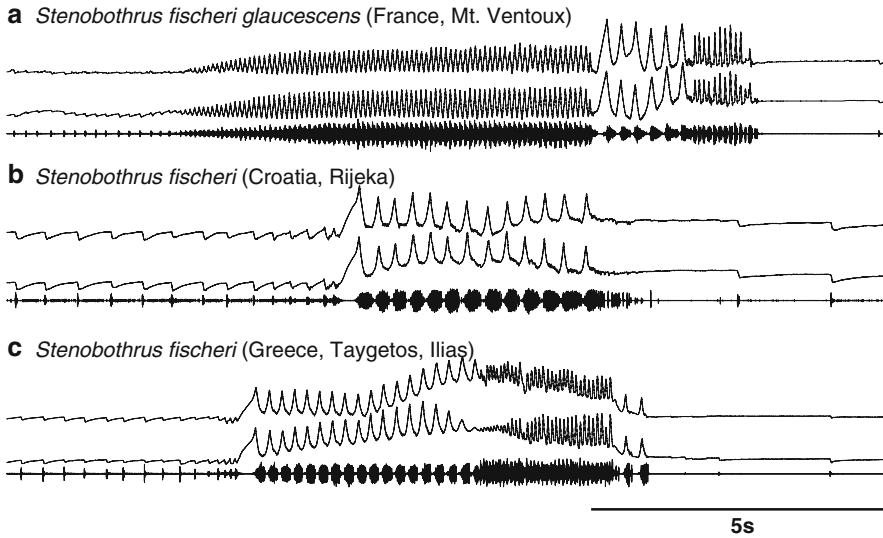
## 1 Introduction

Molecular phylogenetics provides a powerful approach to estimate and compare speciation rates between taxa. Meanwhile, rapid diversification and speciation in some but not in other phylogenetic lineages are well documented in numerous taxa. Despite these advances, the evolutionary mechanisms leading to population divergence and speciation are less clear and require detailed studies of characters involved in reproductive isolation. Such studies have usually concentrated on traits that are directly linked to the ecology of species. A substantial number of studies show how closely related species adapted to different feeding habitats and environments, often after colonization of new areas or the evolution of key innovations. This led to adaptive radiations in numerous taxa. Case studies and evolutionary mechanisms that can cause adaptive radiations were reviewed by Schluter (2000) and Coyne and Orr (2004).

In recent years, it became more and more evident that sexual selection and sexual conflict led to the rapid evolution of prezygotic or premating reproductive isolation (see recent reviews by Ritchie 2007; Snook et al. 2009). This raises two major questions. First, does sexual selection or sexual conflict initiate the evolution of hybridization barriers that could lead to reproductive isolation? Second, does reproductive isolation evolve without a primary role of environmental factors like habitat or food? A positive answer to both questions would support the hypothesis that radiations can occur without a primary role of the environment, i.e., non-ecological radiations.

Grasshoppers of the subfamily Gomphocerinae represent a perfectly suited taxon to test the possibility of non-ecological radiations by rapid divergence of sexually selected traits. Within the family Acrididae only gomphocerine grasshoppers evolved a complex bidirectional acoustic communication system. They produce acoustic signals by rubbing their hind femur against the forewing (e.g., Jacobs 1953; von Helversen and Elsner 1977; von Helversen and von Helversen 1997). The male songs as well as the female acoustic preferences are species-specific and genetically inherited, which resulted in effective premating hybridization barriers (e.g., Perdeck 1958; Stumpner and von Helversen 1994). Several breeding and hybridization experiments among closely related species have shown that premating reproductive isolation evolved prior to obvious postzygotic isolation mechanisms (von Helversen and von Helversen 1975a; Saldamando et al. 2005a, b; Vedenina et al. 2007; Gottsberger and Mayer 2007).

A few lineages of gomphocerine grasshoppers have evolved elaborate acoustic signals. These songs comprise various miscellaneous audible elements, and, in some species, males additionally perform complex visual cues (some examples are given in Figs. 1 and 2). These signals are used in several different behavioral situations, which are all related to mating (for details, see Faber 1953; Jacobs 1953; Alexander 1960; Otte 1970, 1974; Elsner 1974; Ewing 1984; von Helversen 1986). In some species, males produce rivalry songs and respond to each other's songs. The most common songs are male calling songs to which conspecific females respond acoustically when they are willing to mate. The female response song allows the male to locate and approach the female



**Fig. 1** Courtship songs of *Stenobothrus fischeri* males of three allopatric populations. Simultaneous recordings of stridulatory movements of the two hind legs (*upper traces*) using an opto-electronic device (von Helversen and Elsner 1977) and the airborne sound (*lower traces*)

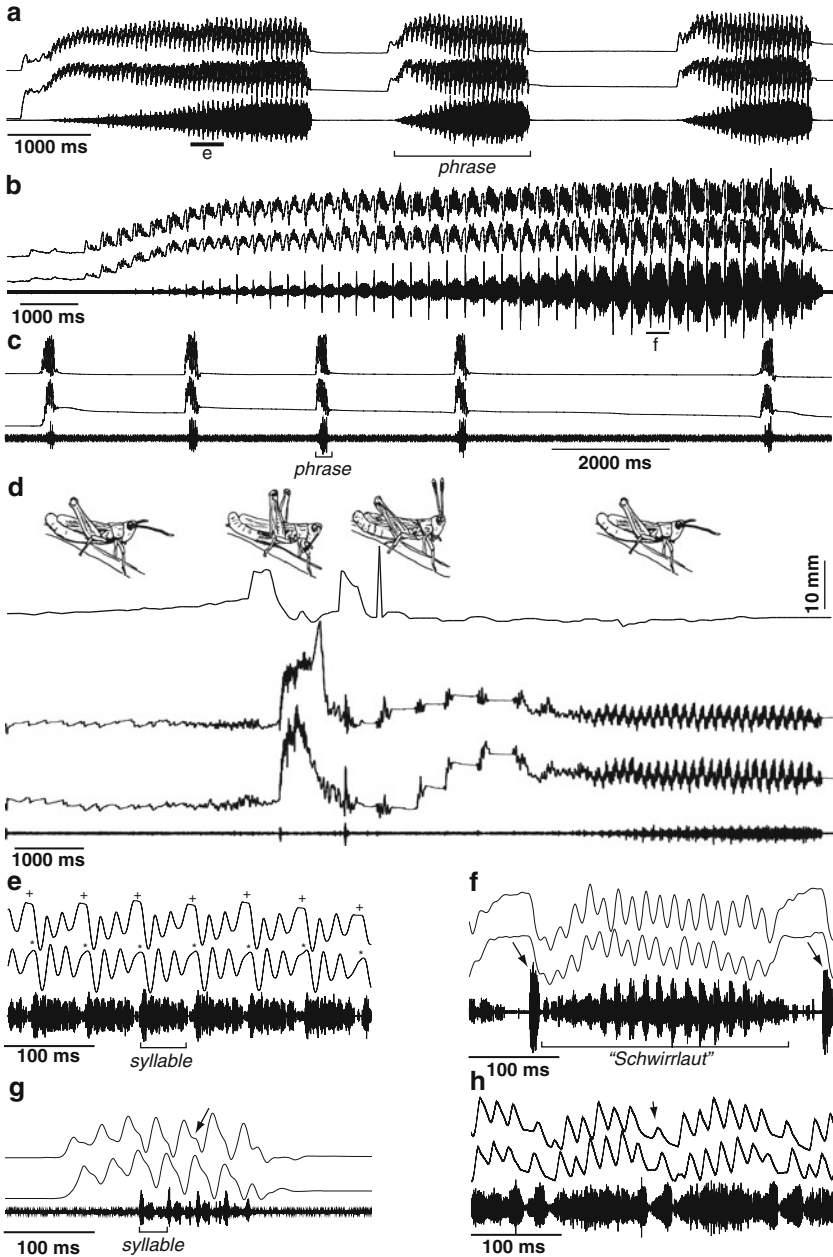
phonotactically (von Helversen 1997). Once they met, the male tries to copulate but a not-excited female can effectively prevent copulations by kicking off the male with the hind legs. Males perform courtship behavior in front of the female to overcome her mating resistance. Therefore, the complex bidirectional communication system of gomphocerine grasshoppers has three major functions: species recognition (von Helversen and von Helversen 1983), mate localization (von Helversen 1997), and sexual selection by female choice (Kriegbaum 1989, Kriegbaum and von Helversen 1992, Klappert and Reinhold 2003).

In this review, we focus on the role of bidirectional acoustic communication for speciation of grasshoppers in the subfamily Gomphocerinae. Female song preferences and co-evolving acoustic mating signals represent intrinsic factors that probably evolve rather independently from the environment. Therefore, ecological factors may not play a crucial role in speciation in acoustically communicating grasshoppers.

## 2 Acoustic Communication and Speciation

### 2.1 Species Diversity and Acoustic Communication

A total of 290 species were listed in a recent survey of grasshoppers of the family Acrididae in Europe (Heller et al. 1998). They are currently classified in seven subfamilies of which the subfamily Gomphocerinae is the most species-rich.



**Fig. 2** Calling songs of *Chorthippus biguttulus* (a, e), *C. mollis ignifer* (b, f), *C. brunneus* (c, g) and *Gomphocerippus rufus* (d, h). Registration of stridulatory movements of the two hind legs (upper traces) and oscillograms of simultaneously recorded airborne sound (lower traces) are shown. Recording temperature was  $31 \pm 2^\circ\text{C}$ . Bars "e" and "f" indicate the details shown in (e) and (f). Arrows in f, g and h mark distinctive parts (for details, see text) of the songs. (a) Male

It comprises almost half the described species (48%). Within the subfamily Gomphocerinae, species diversity is highest in the genera *Chorthippus* and *Stenobothrus* with approximately 45 and 20 species in Europe, respectively (Heller et al. 1998). Both genera comprise a number of species that show highly derived and complex courtship behavior. Such complex courtship behaviors can consist of multiple distinct song elements, which are produced by specific leg movements such as, for example, in *Stenobothrus fischeri* (Fig. 1). In addition, movements of the body, hind legs or antennae can generate visual signals (e.g., Fig. 2; Jacobs 1953; Vedenina and von Helversen 2003).

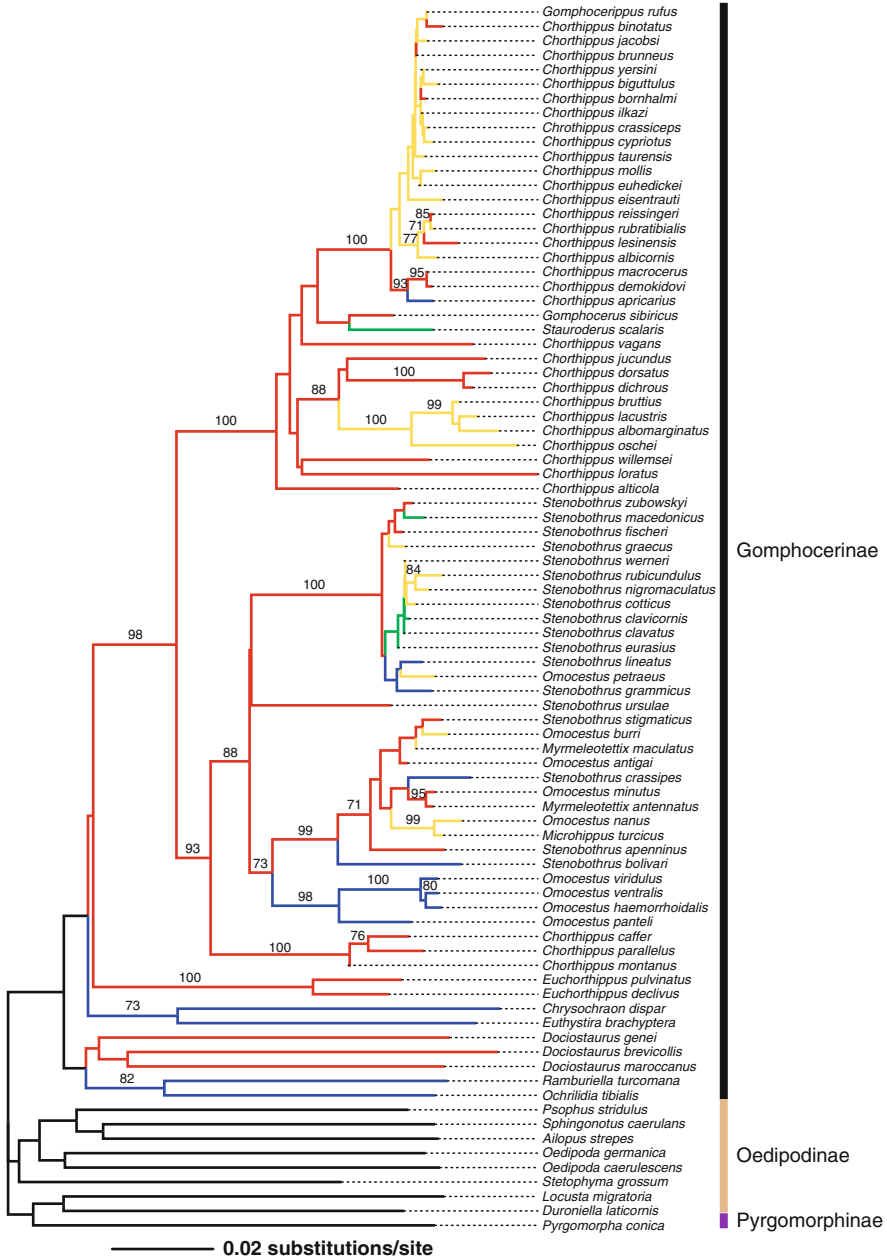
Highest species diversities in the acoustically communicating subfamily Gomphocerinae and in genera that comprise species with complex songs are first indications for a link between acoustic communication and signal complexity with speciation. Unfortunately, analyzing species diversity in different taxonomic groups does not tell one much about the evolutionary time frame in which species diversity evolved. However, a molecular phylogenetic approach allows one to infer speciation rates and to compare them between phylogenetic lineages.

## 2.2 Molecular Phylogeny

The molecular phylogenetic analysis based on the protein coding mitochondrial gene *col* (subunit 1 of cytochrome oxidase) revealed three species-rich lineages (Fig. 3). In all three cases, a long branch leads to a large group of species with similar mitochondrial DNA sequences. One lineage comprises numerous species of the genus *Chorthippus*. The two other lineages include primarily species of the genera *Stenobothrus* and *Omocestus*. The genetic similarity among species (illustrated by short branches in Fig. 3) within these three groups suggests recent and rapid diversification and possibly occasional inter-specific gene flow by hybridization. So far, the incomplete taxonomic sampling prevents calculation of reasonable speciation rates. Nevertheless, the three species-rich lineages comprise species with complex calling or courtship songs (Faber 1953; Jacobs 1953; Raggé and Reynolds

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**Fig. 2** (continued) calling song of *C. biguttulus*. **(b)** Complete *C. mollis ignifer* calling song. **(c)** Calling song of *C. brunneus*. **(d)** Courtship behavior of a *Gomphocerippus rufus* male; in addition to sound (*lower trace*) and leg movements (*middle traces*) the position of the left antenna (*topmost trace*) and characteristic postures (*drawings*) of this species are given. **(e)** Detail of the *C. biguttulus* song shown in **(a)**. The two hind legs are out of phase and perform different movement patterns: one leg (*top trace*) is leading and performs pattern I (+) during the whole phrase; the other leg (*second trace*) is phase-delayed and performs pattern II (\*). **(f)** Detail of the *C. mollis ignifer* song shown in **(b)**. *Arrows* indicate the characteristic pulses of high amplitude at the end of the pause between two “Schwirrlaute”. **(g)** One phrase of the *C. brunneus* song shown in **(c)**. The *arrow* indicates the typical step during the down stroke. **(h)** Detail of the *Gomphocerippus rufus* song shown in **(d)**.



**Fig. 3** Molecular phylogeny of the grasshopper subfamilies Oedipodinae and Gomphocerinae. *Pyrgomorpha conica* (Pyrgomorphinae) and Oedipodinae were used as outgroup. The tree was generated with the Neighbor-joining algorithm and Kimura-2-parameter distances using a 915-bp dataset of the mitochondrial gene *cytochrome oxidase subunit 1 (co1)*. Numbers above branches

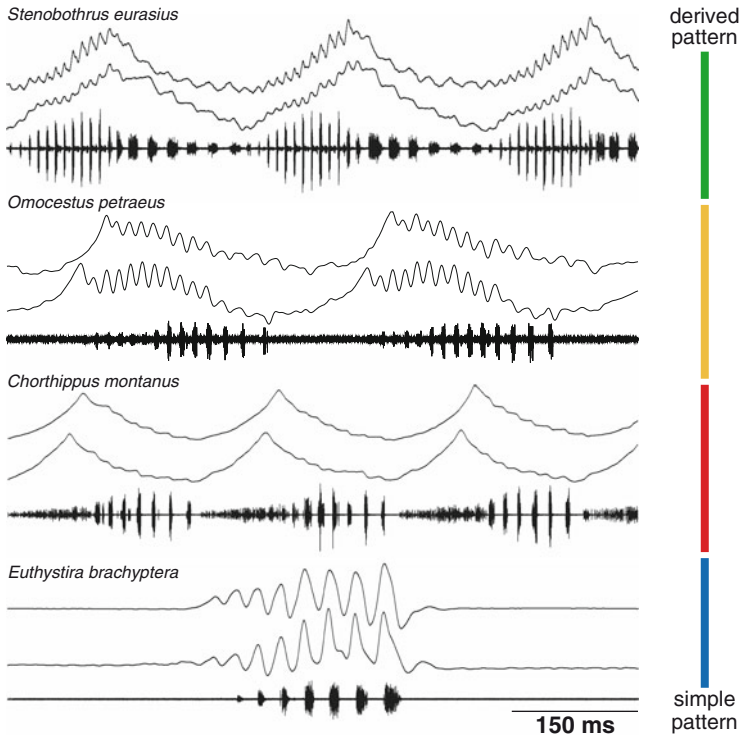
1998; Berger 2008), which supports the hypothesis that song complexity facilitates the divergence of species. This is intuitively not surprising; higher song complexity in terms of complex leg movements, multiple song elements, or visual mating signals in addition to acoustic signals may allow more signal patterns and diverse multimodal signals. Two examples of complex courtship in two distinct lineages are shown in Figs. 1 and 2.

### 2.3 Evolution of Leg Movement Patterns

Gomphocerine grasshoppers reach a high degree of song complexity by the tegmino-femural stridulating mechanism. They typically generate sound by rubbing a row of pegs on the inner side of the femur of each hind leg against a vein of the forewing. Each peg being moved across the forewing causes a very short impulse. A series of impacts, caused by an uninterrupted partial or full up or down movement of a hind leg results in a sound pulse. Pulses are usually separated by pauses. They occur either when the hind leg stops during an up or a down stroke, or when it is at its reversal point from an up to a down stroke or from a down to an up stroke. Series of pulses produced by the right and left hind leg in a specific temporal pattern allow the composition of a great diversity of songs. The increasing complexity can be recognised on different levels, e.g., in structures and substructures of syllables, phrases, and the whole song repertoire (compare Faber 1953; Jacobs 1953; Otte 1970; von Helversen and von Helversen 1994).

Elsner (1983) provided the first contribution to the phylogeny of stridulatory motor patterns, and von Helversen and von Helversen (1994) proposed a successive increase of complexity in leg movements. Basal lineages of gomphocerine grasshoppers (Fig. 3) produce series of simple (uninterrupted) up and down strokes of both hind legs. Such a presumably plesiomorphic leg movement pattern is found, for example, in the genera *Ochrilidia*, *Euthystira*, and *Chrysochraon*. Sound could be emitted during up and down strokes or only during down strokes (e.g., Fig. 4). It is conceivable that these simple leg movements descend from locomotion or defence movements (Faber 1953; Jacobs 1953). A number of genera including *Dociostaurus*, *Omocestus*, *Stenobothrus*, and *Chorthippus* generate characteristic song elements (often called syllables; e.g., Ragge and Reynolds 1998) by leg movements with straight up and stepped down strokes (compare Stumpner and von Helversen 1994; Ragge and Reynolds 1998; Berger 2008). This suggests that, early in song evolution of gomphocerine grasshoppers, the continuous down stroke

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**Fig. 3** (continued) refer to bootstrap support values of at least 70. Poor resolution close to the root is likely the result of homoplasy due to relatively high mutation rates of the mitochondrial genome. In contrast, the *short branches* close to the *tips* suggest recent divergence and thus rapid speciation (radiations) in some but not other lineages (for details, see text)



**Fig. 4** Four levels of leg movement complexity (modified from von Helversen and von Helversen 1994). Straight up and down strokes (*Euthystira brachyptera*-pattern), straight up and stepped down strokes (*Chorthippus montanus*-pattern), straight up and vibratory down strokes (*Omocestus petraeus*-pattern) and stepped up and stepped down strokes (*Stenobothrus eurasius*-pattern). For each recording leg movements (upper traces) and oscillogram of the emitted sound (lower trace) are given. The colors correspond to those in the phylogenetic tree shown in Fig. 3

became interrupted by short stops during the down movement. This results in series of short pulses during the down stroke, whereas during the up stroke one longer pulse is emitted (e.g., *C. montanus*; Fig. 4). The stepped down stroke was presumably an important initial development that led to the impressive diversity of complex songs. In many species, the stops during the down stroke evolved into a short up movement. This resulted in high frequency vibratory movements during the down stroke and series of short pulses arose. *Omocestus petraeus* (Fig. 4), *Stenobothrus nigromaculatus* and *Myrmeleotettix* spp. (Elsner and Popov 1978; Berger 2008) are nice examples for this trend. In *Stenobothrus eurasius*, complexity increased by the adoption of faster vibrations, also during the up stroke, which resulted in shorter pulses during the up stroke and longer pulses during the down stroke (Fig. 4).



## 2.4 Song Evolution in Closely Related Species

In order to illustrate the evolution of strikingly different songs within a group of closely related species, we selected the well-studied species group of *Chorthippus biguttulus*. The three species, *Chorthippus biguttulus*, *C. brunneus* and *C. mollis*, occur in sympatry across wide areas in Europe (Ragge et al. 1990). They closely resemble each other in their external morphology suggesting a close relationship. This is supported by the similarity of mitochondrial DNA sequences (Mason et al. 1995; see above).

The male calling song of *Chorthippus biguttulus* (Fig. 2a, e) is a well-known example of the asynchronous co-ordination of both hind legs. The phase shift between legs masks pauses: while one hind leg generates a pulse, the other leg is at its turning point. The resulting prolonged sound elements are often referred to as syllables (Jacobs 1953; von Helversen 1972; von Helversen and von Helversen 1997). The proportion of syllable duration to the pause between the syllables is the most important factor for the innate releasing mechanism of the females (von Helversen 1972; Gottsberger 2007). The syllables are repeated many times resulting in a higher-level song element, often referred to as a phrase (e.g., von Helversen and von Helversen 1997). As with other song elements, phrases are repeated several times forming a song (Fig. 2a).

In contrast to *C. biguttulus*, *C. mollis* produces whirr-like elements called “Schwirrlaute” (Fig. 2f). These “Schwirrlaute” are repeated many times (up to more than 100) to form a song (Fig. 2b). Within the pause between two “Schwirrlaute”, a strong down stroke of at least one leg causes an isolated prominent pulse (see arrows in Fig. 2f). Hybridization experiments between *C. biguttulus* and *C. mollis* indicate that “Schwirrlaute” are not homologous to “*C. biguttulus*-syllables” (for details, see von Helversen and von Helversen 1975a).

The calling song of *Chorthippus brunneus* has a characteristic phrase structure that differs conspicuously from those of *C. biguttulus* and *C. mollis* (Fig. 2c). The 5–14 phrases last only about 180 ms and each phrase is usually generated by five leg movement cycles (compare Fig. 2g), each of them producing a syllable. Each syllable is generated by three step leg movement cycle: i.e., one continuous up stroke and a two-step down stroke (Gottsberger and Mayer 2007).

The analysis of mitochondrial DNA sequences suggests that *Gomphocerippus rufus* is also closely related to the species mentioned above. The male performs a conspicuous courtship display in front of the female (Fig. 2d). It starts with primarily visible elements like head wagging, antennal movements, high amplitude leg movements, and two short acoustic pulses. The clubbed antennae with high-contrast tips, the light mouthparts, and reddish hind legs are certainly associated with this behavior. Thereafter, the major sound element follows. It resembles the calling song and comprises two elements performed in alternation as in *C. mollis* calling songs. The first element is a relatively loud pulse caused by a down stroke of both hind legs (see arrow in Fig. 2h). Thereafter, a vibratory element of about six leg movement cycles follows. All in all, the leg movement patterns of

all these four closely related species resemble highly complex stridulation patterns that result in very different songs.

### 3 Mechanisms of Speciation

The phylogenetic approach and detailed song analyses do not allow one to infer and distinguish between different mechanisms of speciation. Therefore, the question remains how populations diverge and how this can lead to reproductive isolation. At least two mechanisms contribute to population divergence and the evolution of new songs.

#### 3.1 Divergence in Allopatry

The recent radiation of Gomphocerinae is supposed to be a result of divergent evolution of partial populations by geographic separation induced by climatic oscillations during the Pleistocene. Thermophilic species – as are most Gomphocerinae – were restricted to southern refuges during glacial stadials, in Europe, the Iberian Peninsula, the Apennine Peninsula, and the Balkans (Taberlet et al. 1998; Hewitt 1999). During the warm interstadials, they expanded their ranges northwards. In contrast, cold-adapted species, mainly montane, alpine, and boreo-alpine species, survived glacial maxima in lower altitudes and show currently disjunctive distributions (Ramme 1951; Berger et al., 2010).

Many widespread species with a continuous distribution throughout Europe show no or little differences in their calling and courtship songs, e.g., *Chorthippus parallelus*, *C. vagans*, *C. montanus*, *Omocestus ventralis*, *O. haemorrhoidalis*, *Stenobothrus stigmaticus*, and *S. lineatus* (Ragge and Reynolds 1998; own unpublished data). In contrast to these species, *Stenobothrus fischeri* is an example for a gomphocerine species with a fragmented distribution over a wide range of southern Europe (Harz 1975). Across the whole distribution range, calling songs do not show obvious differences. The song consists of short phrases of about 2–4 s and syllables are produced by leg movement patterns, which are very similar to those of *Chorthippus montanus* (Fig. 4; Berger 2008). In contrast to calling song, the courtship song consists of up to four different song elements as in western populations of *Stenobothrus fischeri* (Fig. 1a; Berger 2008): a series of “ticking” pulses prelude the courtship song. The second element resembles a prolonged calling song phrase. The third element consists of a series of syllables that are produced by highly elevated leg movements. The highly elevated movements of the hind legs (which are conspicuously marked by darkened knees) likely represent a visual stimulus. The fourth element (ritualised pre-mounting jumping strokes) is produced by highly excited males at the very end of a courtship by a series of fast leg strokes that result in sharp pulses.

In contrast to the western populations of *S. fischeri*, the populations from Croatia and Greece lack the second (the calling song-like) element (Fig. 1; for further details, see Berger 2008). These obvious differences in courtship songs of geographically separated eastern and western populations of *Stenobothrus fischeri* populations suggest that the ancestral *S. fischeri* already produced multi-component courtship songs, comprising all four elements. *Stenobothrus fischeri* illustrates that complex songs in terms of multiple song elements and/or multimodal courtship can lead to rapid divergence in geographically separated populations. Nevertheless, it is unclear to which degree selection, novel mutations, or genetic drift contribute to this divergence.

### 3.2 Evolution of New Songs by Hybridization

Interspecific hybrids and more or less wide hybrid zones were reported from a number of taxa particularly in the genus *Chorthippus*. These hybrids were commonly recognized according to their characteristic and unique calling songs. The analysis of hybrid songs often revealed intermediate song parameters in hybrids. Songs of *Chorthippus p. parallelus* and *C. p. erythropus* differ mainly in the duration of syllables within a phrase. Male hybrids between the two taxa produced songs with an intermediate phrase duration, probably formed by a simple introgression of characters (Butlin and Hewitt 1985a, b). Songs of hybrids between *C. brunneus* and *C. jacobsi* were also intermediate for the characters phrase duration (called “echeme”), syllable duration (called “phrase”), and pulse duration (called “syllable” in Saldamando et al. 2005a). In contrast, the analysis of *C. biguttulus* and *C. mollis* hybrids showed that songs of F1 hybrid males were generated by more complex leg movement patterns than observed in both parental species because hybrids produced leg movement patterns of both species (von Helversen and von Helversen 1975a). Meanwhile, natural hybrids between *C. biguttulus* and *C. mollis* were found, which also showed the combination of parental song parameters of both parental species (own unpublished data). A similar observation of increased complexity in hybrid songs was made in hybrids between *C. albomarginatus* and *C. oschei*. These two parental species have elaborate songs with a conspicuous visual display. The hybrids show more complexity in songs, and moreover even include novel elements in their courtship displays (Vedenina et al. 2007). Different leg movement patterns could possibly be combined in hybrids if two independent neuronal pattern generators are responsible for the different leg movement patterns. Such a neuronal control may allow for both networks being expressed in hybrids and lead to a common final output (von Helversen and von Helversen 1975b; von Helversen and Elsner 1977). Novel songs were also observed in hybrids between *C. biguttulus* and *C. brunneus*. But these hybrids showed more simple songs than the parental taxa. The distinct temporal patterns of syllables and pulses within phrases of the parental species got lost and resulted in uniformly performed up and down movements of legs in the hybrid songs (Gottsberger and

Mayer 2007). This indicates that the neuronal networks of *C. biguttulus* and *C. brunneus* cannot be formed in parallel. These studies of currently hybridizing taxa show that hybridization can rapidly lead to novel songs. Thus, hybridization could have been one factor for speciation in grasshoppers.

## 4 Conclusions

In gomphocerine grasshoppers, the bidirectional communication system plays a major role in reproductive isolation between species, since other mechanisms (e.g., complex genital apertures or obvious post-mating hybridization barriers) are not developed among recently diverged species. The willingness of females to mate depends on the male's calling and courtship behavior. The evolution of complex species-specific acoustic signals that were complemented by visual signals in several lineages contributed to independent radiations in different clades. Although the underlying evolutionary mechanisms are not well understood, ethological differentiation at least during geographic separation and hybridization after secondary contact of populations has contributed to new song patterns. It is unknown to what degree ecological factors may have influenced species diversity. Songs may also have been influenced among sympatrically occurring grasshopper species (Bukhvalova and Zhantiev 1993; Safi et al. 2006). Nevertheless, rapid evolution of effective premating barriers in gomphocerine grasshoppers in terms of strong female preferences for conspecific males' courtship behavior represents a promising candidate for non-ecological radiations.

**Acknowledgements** We thank Jana Ustinova and Klaus-Gerhard Heller for fruitful discussions and important suggestions for the manuscript. The Deutsche Forschungsgemeinschaft (DFG) and the Staedtler-Foundation supported our work financially.

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