

# Asymmetric mate choice, hybridization, and hybrid fitness in two sympatric grasshopper species

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**Abstract** Hybridization between animal species has long been regarded as unusual, but is meanwhile accepted as a widespread phenomenon. Typically, sexual interactions among species are studied in secondary contact zones of closely related species (hybrid zones) or between invasive and native species, whereas hybridization between sympatric congeners has received little attention. Here, we present a study on the hybridization potential of two grasshopper species, *Chorthippus parallelus* and *Chorthippus montanus*, which occur sympatric in large parts of Eurasia. We performed a mate choice experiment with specimens from an area of local parapatry in northwestern Germany. Most copulations were conspecific, but males of both species and females of *C. parallelus* were indiscriminate in their mate choice, while females of *C. montanus* clearly preferred conspecific males. Although these results suggest asymmetric introgression, a no-choice hybridization experiment revealed that hybridization is possible in both directions. The hatching success of the hybrids was intermediate between the parental species. Female hybrids showed no clear mate preferences, indicating that back crossing in both directions is possible in principle, but the fertility of the hybrids and the fitness of the F2 generation remain unknown. Our study suggests that hybridization between

sympatric species might occur more often than assumed. It might affect the ecology and local distribution of animals in a similar way as competition does.

**Keywords** Assortative mating · Coexistence · Introgression · Reproductive interference · Mate choice · Orthoptera

## Introduction

Hybridization has long been regarded as an unusual phenomenon (Mallet 2005), creating problems for taxonomists and ecologists who need discrete units for describing, assessing, and understanding biodiversity patterns. Despite or even because of this, the phenomenon has attracted much attention by evolutionary biologists (e.g., Barton and Hewitt 1985; Rhymer and Simberloff 1996; Wirtz 1999). Hybrids or their offspring might have only a slightly lower fitness or are completely inviable, and premating barriers might lead to a partial or complete reproductive isolation (Pfennig 2007; Mallet 2008). Moreover, hybridization and introgression seem to be common patterns in phylogenetic analyses at genus level (e.g., Grant et al. 2005). The ecological consequences of hybridization and other types of reproductive interference (signal jamming during mate finding, heterospecific courtship, interspecific territoriality, mating attempts, etc.) have become a rapidly growing field of research (Ribeiro and Spielman 1986; Kuno 1992; Hochkirch et al. 2006; Liu et al. 2007; Gröning and Hochkirch 2008). The ecological impact of sexual interactions between species is caused by the potentially high fitness costs to at least one sex of the species involved. Thus, reproductive interference might ultimately lead to displacement of this species (“sexual exclusion,” Hochkirch et al. 2007a). Traits that reduce these costs might, therefore, be

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positively selected and lead to reinforcement of premating barriers (Dobzhansky 1937; Spencer et al. 1986; Butlin 1989; Servedio and Noor 2003) or drive the ecological divergence of species (Kawano 2004; Gröning and Hochkirch 2008).

So far, the majority of hybridization studies has focused on narrow suture zones, in which parapatric species pairs came into secondary contact (reviewed in Barton and Hewitt 1989; Buggs 2007), while studies on sympatric species pairs are relatively sparse (but see Coyne and Orr 1989, 1997). The assumption in such situations is usually that hybridization must be rare as otherwise, the species could not persist in sympatry. Recently, interactions between invasive and native species have become another major area of hybridization research, as some introduced species seem to displace their native relatives (e.g., Liu et al. 2007; Kanbe et al. 2008). Species with broadly overlapping ranges are still often thought to be unlikely to interact sexually as their specific mate recognition system (SMRS) should have evolved in response to such interactions (Paterson 1985). However, it has been shown that reproductive interference also frequently affects the coexistence of sympatric species (Gröning and Hochkirch 2008). One possible explanation could be that sympatric species do not necessarily come into direct contact as they might have allotopic distribution patterns, which means that they occur in different habitat types or simply at different sites within the same range (Gröning and Hochkirch 2008). If such species pairs come into contact occasionally, mosaic hybrid zones could emerge (Harrison and Rand 1989; Bailey et al. 2004). It is possible that in each zone of secondary contact, natural variation in courtship traits, preference traits, or ecological attributes might give rise to different patterns of sexual interactions. In some cases, hybridization might be rare due to little temporal or spatial overlap of two populations, while in other populations, hybridization could be a common phenomenon or might even be associated with an increased fitness rather than with costs (Fitzpatrick and Shaffer 2007; Pfennig 2007). We, therefore, need a better understanding of the nature and extent of hybridization in sibling species pairs with overlapping distributions.

An important model system for hybridization is the grasshopper species *Chorthippus parallelus* (Zetterstedt, 1821), which has been studied in a hybrid zone of two subspecies in the Pyrenees (Butlin and Hewitt 1985a, b; Ritchie et al. 1989; Virdee and Hewitt 1990; Butlin and Ritchie 1991; Bella et al. 1992; Buno et al. 1994; Dagley et al. 1994; Butlin 1998). In large parts of its range, *C. parallelus* also occurs sympatrically with another sibling species, *Chorthippus montanus* (Charpentier, 1825), which has been suggested to represent “a potentially significant environmental factor” for *C. parallelus* (Tregenza et al. 2000a, b). *C. montanus* is morphologically rather similar to

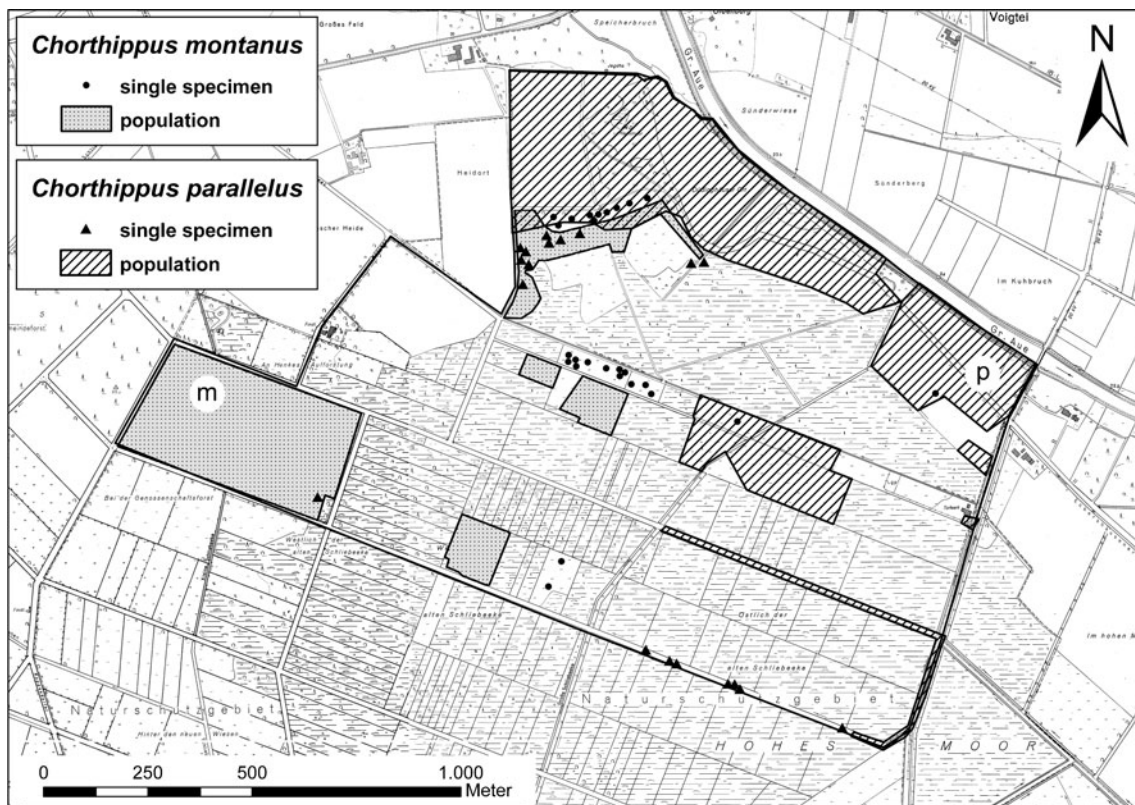
*C. parallelus*, has a similar song, and has similar cuticular hydrocarbons (Reynolds 1980; Bauer and von Helversen 1987; Rague and Reynolds 1998; Tregenza et al. 2000b). The main difference between the two species is found in their ecology: *C. montanus* is strongly associated with wet grasslands, whereas *C. parallelus* occurs in a variety of grassland habitats, including dry and wet sites (Detzel 1998). Sexual interactions between these two species have never been studied in detail, although they are known to hybridize in the laboratory (Bauer and von Helversen 1987) and probably also do so in nature (Reynolds 1980). *C. parallelus* occurs sympatrically with *C. montanus* almost throughout the complete range of the latter species (Kleukers et al. 1997).

During a mapping project in 2001, we detected a local contact zone between *C. montanus* and *C. parallelus* in a disturbed peat bog in northwestern Germany (Fig. 1, for detailed information on the study area, see Hochkirch and Adorf 2007; Hochkirch et al. 2007b; Witzemberger and Hochkirch 2008). While *C. parallelus* occurred on grasslands and trails in the north and east of the bog, *C. montanus* was found in similar habitats in the western part of the study area. Only a narrow zone of overlap was detected at the northwestern edge of the bog, but single (macropterous) individuals of both species were found in the center of populations of heterospecifics. In the center of the study area, populations of both species are divided by unsuitable habitat (birch woods). This pattern of local parapatry was somewhat surprising as the two species are also known to co-occur at other sites (Tregenza et al. 2000b) and as herbivorous species are unlikely to compete for resources (Strong et al. 1984). Indeed, food (grasses) and oviposition sites (soil) are abundant in the habitat of the two species. It is also unlikely that this pattern is caused by niche differences as the grasslands in the eastern and western parts of the bog did not differ in management, vegetation, or soil moisture (unpublished data). In 2006, we started a project to test whether sexual interactions could be a reason for the pattern of local parapatry. Specifically, we wanted to know if reproductive interference occurs between the two species. If reproductive interference was found, we wanted to analyze whether it was asymmetric. Moreover, we wanted to test the hybridization potential and the fitness of the hybrids in terms of hatching success. Third, we were interested in the mate preferences of the hybrids in order to assess the backcrossing pattern and possible pathways of introgression.

## Method

### Study species

*C. parallelus* is a common grasshopper species that occurs in a variety of grassland habitats, including pastures,



**Fig. 1** Local distribution of *Chorthippus montanus* and *Chorthippus parallelus* in the study area, a disturbed peat bog in northwestern Germany. The two species occur in local parapatry with a contact zone

in the north of the study area. The circles show where specimens for the experiments have been collected (m: *C. montanus*, p: *C. parallelus*)

meadows, fallows, fens, and fringes of ditches or roads, but it is missing in wooded habitats (Detzel 1998). The species is distributed over large parts of Europe and Asia (Kleukers et al. 1997) and feeds on a variety of grasses (Ingrisch and Köhler 1998). *C. montanus* is found from Western Europe to Kamchatka. Both species occur sympatrically throughout nearly the complete range of *C. montanus* except for northern Sweden. In Germany, both species are widespread, but *C. montanus* is associated with wetlands (mainly mesotrophic turf fens). Both species are univoltine; they reproduce from July to September and hibernate in the egg stage (Kleukers et al. 1997). *C. montanus* becomes adult slightly later than *C. parallelus*, probably due to the cool microclimate of its habitat (own observations). The songs of both species are rather similar, but *C. parallelus* produces fewer syllables per echeme and has a faster syllable repetition rate (Reynolds 1980; Bauer and von Helversen 1987). The species are known to hybridize in the laboratory (Bauer and von Helversen 1987), and based on individuals with intermediate traits, it has also been suggested that hybrids are found in nature (Reynolds 1980).

#### Mate choice experiment

Nymphs of the two species were collected on 20 June, and 2 and 5 July 2007 in the study area (Fig. 1). We collected >90 male and female nymphs of each species on sites where only one species was present (*C. parallelus*: 52°36' 2.04"N, 8°54'4.26"E; *C. montanus*: 52°36'0.46"N, 8°52' 22.61"E, Fig. 1). The sexes and species were kept separately in plastic containers (15×26×19 cm) with a moist sand-covered floor (2–3 cm high, five containers per sex and species). They were kept in a greenhouse of the University of Osnabrück with a daily temperature of 27°C and a nocturnal temperature of 15°C. The relative humidity was 50–55%. The insects were fed with different grasses, which were replaced every second day (*Dactylis glomerata*, *Holcus lanatus*, *Poa annua*, *Poa trivialis*, and *Agrostis gigantea*), and the boxes were kept moist with a spray flask. The mate choice experiments were performed 2 weeks after the last insects became adult, from 10 July to 2 August 2007 between 9 a.m. and 6 p.m. The conditions were similar to the housing conditions, but four additional overhead lights (Osram Universal White Light, light color

25, 58 W) and two halogen spotlights (15 W) at 30 cm distance were used to illuminate the terrarium. We placed one individual (20 replicates for each sex and species) together with one conspecific and one heterospecific mate in the terrarium and noted their behavior every 30 s for 30 min. Afterwards, we checked the terrarium for another hour every 15 min to note copulations. On average, copulations of *C. parallelus* are known to last 37 min (Reinhardt 2001). Hence, it is rather unlikely that we have missed a copulation. To avoid effects of the diurnal activity pattern, we started each day with a different treatment in an alternating order (Hochkirch et al. 2008). In order to analyze mate preferences, we summarized all observations of directed movements (“approaches”) of each sex (locomotion, male courtship, female response stridulation, and mating attempts) to each potential mate (observations every 30 s, see above). Locomotion was only counted as a mate preference parameter if the insect directly walked or jumped to the potential mate in response to a male or female behavior and subsequently touched the other insect. The individuals were placed in a separate terrarium afterwards to avoid pseudoreplication.

#### Hybridization experiment

To study the fitness of hybrids in comparison with *C. montanus* and *C. parallelus*, we performed a hybridization experiment in the laboratory. On 4 July 2006, we collected 20 nymphs of each species and sex at the sites mentioned above. We performed four treatments with different species composition, each of which was replicated three times. In each terrarium, we placed two males of one species together with two conspecific females (control) or with two heterospecific females. The experimental conditions were similar to those in the mate choice experiment, but the boxes were filled with 5 cm of soil for oviposition. From 19 September 2006 onwards, we stepwise reduced the diurnal temperature to 10°C and hibernated the eggs outdoors. The containers were watered each week and brought to the greenhouse again in March 2007 (diurnal temperature 20°C, nocturnal temperature 10°C). Hatching started on 11 April, and the hatching success was recorded from this date onwards. We used the maximum number of hatchlings in each container (reached on 18 April 2007) for the analyses. Dead hatchlings were not recorded before this date, suggesting that no individuals have been missed. Males and females from each terrarium were separated on the day of the final molt to avoid copulations.

#### Hybrid mate preferences

To analyze the mate preferences of the hybrid offspring, we conducted a mate choice experiment for hybrid females.

The number of adult hybrid males was too low to perform a similar experiment. The mate choice experiment was performed from 15 to 28 June 2007 between 9 a.m. and 6 p.m. The conditions were similar to those mentioned above, but only one halogen spotlight (15 W) was used. We placed each hybrid female (seven *C. parallelus* F × *C. montanus* M and six *C. montanus* F × *C. parallelus* M) together with two males (one *C. parallelus*, one *C. montanus*) in a terrarium and noted their behavior every 30 s for 30 min. Again, we checked the terrarium for another hour every 15 min to note copulations. If a copulation occurred, we stopped the observation. Due to the small sample size of adult hybrids, we repeated the treatment for each female with different male pairs until it copulated. One specimen (*C. montanus* F × *C. parallelus* M) did not copulate at all.

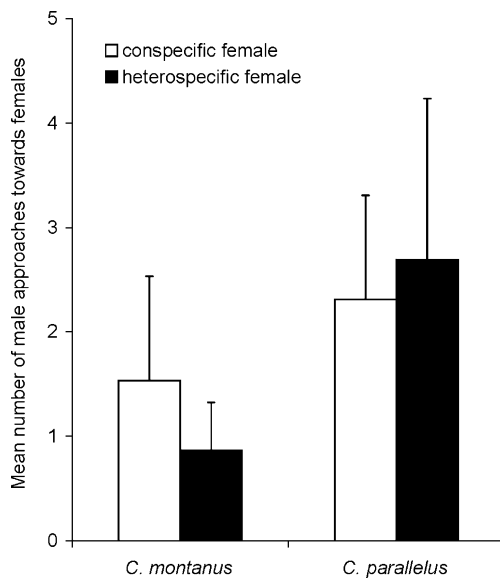
#### Statistical analysis

To test for interspecific differences in mate choice, we used a generalized linear model (binomial error distribution) with “species” as the explanatory variable and mate choice scores (1 for conspecific mate and 0 for heterospecific mate) as response variable. We used generalized linear models (GLM) with a binomial distribution to test for interspecific differences in mate preferences. For testing hybrid mate preferences, we scored according to the chosen male (*C. parallelus* male=1 and *C. montanus* male=0). To test for differences in the hatching success in the four treatments of the hybridization experiment, we used a repeated measures ANOVA with “number of nymphs” as the response variable and with “treatment” (two conspecific and two hybridization treatments) and “date” as the explanatory variables. All statistic analyses were performed with “R 2.8.0” (R Development Core Team 2008).

## Results

#### Mate choice experiments

Males of the two species did not discriminate between conspecific and heterospecific females (GLM,  $z=-0.282$ ,  $df=27$ ,  $P=0.78$ ; Fig. 2). Females of *C. montanus* approached conspecific males to a much higher proportion than heterospecific males, while *C. parallelus* females showed no differences between males of each species (GLM,  $z=-2.533$ ,  $df=21$ ,  $P=0.01$ ; Fig. 3). Most copulations were conspecific, but we observed two heterospecific copulations of *C. montanus* males (total, nine copulations) and one copulation between a *C. parallelus* male and a *C. montanus* female (total, seven copulations). The observed females performed

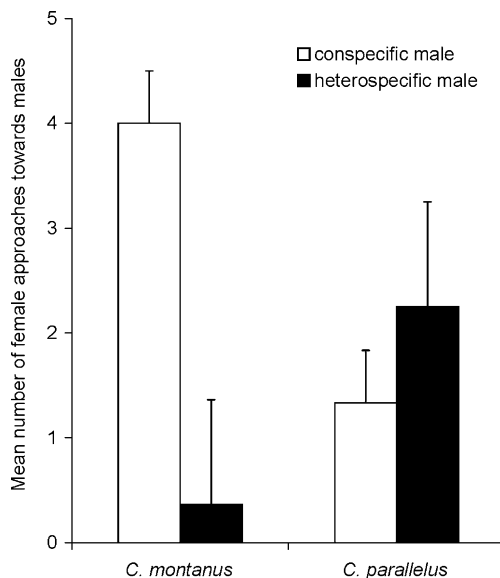


**Fig. 2** Male mate preferences of *Chorthippus montanus* and *Chorthippus parallelus* in mate choice experiments with one female of each species. Error bars are standard errors

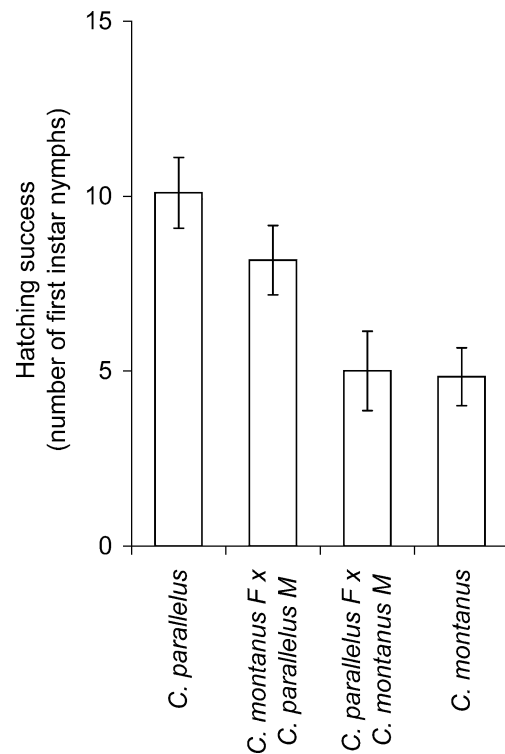
only conspecific copulations (*C. parallelus*, ten copulations; *C. montanus*, 13 copulations).

#### Hybridization experiment

Nymphs hatched from all treatments of the hybridization experiment. The number of nymphs was significantly lower in *C. montanus* than in *C. parallelus* (repeated measures ANOVA,  $F_{3,8}=11.42$ ,  $P<0.001$ ; Fig. 4). In the



**Fig. 3** Female mate preferences of *Chorthippus montanus* and *Chorthippus parallelus*. Error bars are standard errors



**Fig. 4** Mean number of first instar nymphs of *Chorthippus parallelus*, *Chorthippus montanus*, and their hybrids on the day of maximum nymph abundance (18 April 2007). Error bars are standard errors

hybrid treatment *C. montanus* F × *C. parallelus* M, an intermediate number of first instar nymphs hatched, while in the reverse treatment, the number of nymphs was rather similar to *C. montanus*. The survival rate of the nymphs was extremely variable within treatments (between 0% and 100%), but did not differ amongst the treatments (on average 65% survival; repeated measures ANOVA,  $F_{3,8}=0.38$ ,  $P=0.77$ ). Fifteen hybrid males and 14 females reached the adult stage. Nearly all hybrid males had wing deformations rendering them unable to sing. Thirteen hybrid females could be used to test the hybrid mate preferences.

#### Hybrid mate preferences

Both hybrid types did not discriminate between males of the two parental species (GLM,  $df=11$ ,  $P=0.92$ ). *C. parallelus* F × *C. montanus* M hybrids performed four copulations with males of *C. parallelus* and three with *C. montanus*. The second hybrid type (*C. montanus* F × *C. parallelus* M) copulated three times with males of *C. parallelus* and two times with *C. montanus* males. Both hybrid types showed an equal number of approaches towards males of the two species (ten approaches to *C. parallelus*, ten to *C. montanus*).

## Discussion

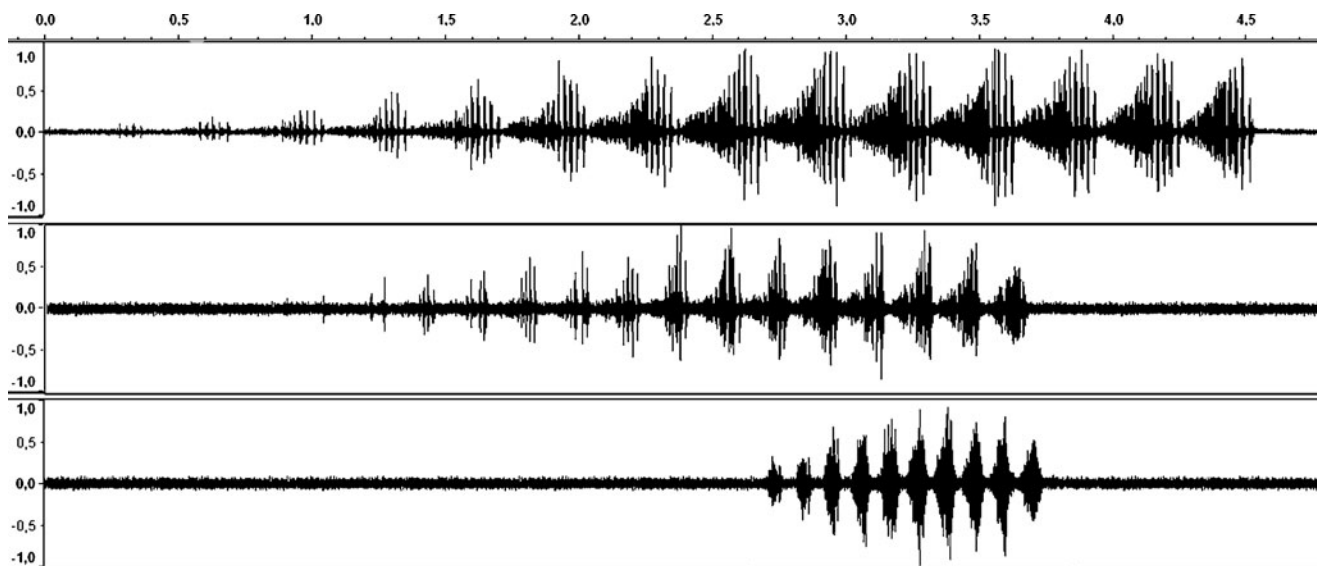
### Hybridization potential

Our results show that *C. parallelus* and *C. montanus* readily hybridize in no-choice experiments and that only females of *C. montanus* discriminate clearly between conspecific and heterospecific males in mate choice experiments (although all copulations were conspecific). The number of hatched hybrids was intermediate compared to the parental species, but most adult hybrid males had wing deformations. However, as many individuals were macropterous, the keeping conditions might have influenced wing development (Poniatowski and Fartmann 2009). As the stridulatory organs of Gomphocerinae grasshoppers are located on the wings and the songs are important traits for mate choice (Ragge and Reynolds 1998), wing deformations could possibly decrease the fitness of many hybrid males. Only one adult hybrid male with normally developed wings was obtained (*C. parallelus* F × *C. montanus* M), which had intermediate song characteristics (Fig. 5). It remains unclear if this would further decrease the fitness of male hybrids as the response of females to hybrid songs has not yet been studied. Ritchie (1990) argues that the importance of song differences for species recognition might be overstated as other modes of communication might be less apparent than the song but more important for mate acquisition (e.g., olfactory traits). However, in mate choice experiments with *Chorthippus parallelus erythropus*, he found a strong influence of the song on the mate choice of *Chorthippus parallelus parallelus*, a pattern that was confirmed by field

observations (Neems and Butlin 1993) and that is also known from other *Chorthippus* species (von Helversen 1972; Klappert and Reinhold 2003; Gottsberger and Mayer 2007). On the other hand, geographic variation in the male calling song among European populations of *C. parallelus* is not related to the level of premating isolation (Tregenza 2002). Since in our experiment *C. parallelus* females did not discriminate between males of the two parental species, it seems reasonable to suggest that they also would not discriminate against hybrid males.

### Preferences of female hybrids

In contrast to the males, female hybrids showed no noticeable anomalies suggesting a reduction in fitness compared to non-hybrid females, a pattern that is in good accordance with Haldane's rule (Haldane 1922) and that has also been reported from the Pyrenean hybrid zone of *C. parallelus parallelus* and *C. parallelus erythropus* (Hewitt et al. 1987; Butlin and Hewitt 1988). As female hybrids had no preferences for one of the parental species, they might backcross in both directions, but it should be noted that the backcrossing potential (i.e., the fertility of hybrids) and the fitness of the F2 generation still remains unstudied. In other studies, the preference of pure individuals for either pure or hybrid males was tested. These studies showed conflicting results. In *Chorthippus albomarginatus* and *Chorthippus oschei*, no preference for pure or hybrid males was found (Vedenina et al. 2007), while female hybrids of *Chorthippus brunneus* and *Chorthippus jacobsi* preferred parental over hybrid songs (Bridle et al. 2006).



**Fig. 5** Oscillogram of the male calling song of *Chorthippus montanus* (upper graph), *Chorthippus parallelus* (lower graph), and a hybrid (*C. parallelus* F × *C. montanus* M, central graph). The songs were recorded with a digital audio recorder (Marantz Professional solid-state

recorder PMD 660) and a shotgun microphone (Sennheiser ME-66, powering module: Sennheiser K6) in a glass terrarium at a temperature of 31–33°C (27 July 2007, 11 a.m.–2 p.m.)

Bauer and von Helversen (1987) mention that hybrid females of *C. parallelus* and *C. montanus* prefer hybrid songs, but Butlin and Hewitt (1986) argue that in nature, the majority of matings are the result of initial chance contacts. A preference for a particular song pattern might therefore be misleading, as the female response stridulation and phonotaxis seem to be mainly important at low population densities (Butlin and Hewitt 1986). Hence, our mate choice experiment might be more reliable in simulating the natural condition as it includes both songs and encounters. On the other hand, unnatural high densities (i.e., unnatural high heterospecific encounter rates) in experimental arenas might also influence the outcome of mate choice experiments (Gröning et al. 2007).

#### Asymmetric mate choice and introgression

Our experiment revealed a strongly asymmetric pattern of mate choice. While females of *C. montanus* were rather choosy, females of *C. parallelus* and males of the two species did not discriminate between conspecific and heterospecific mates. The widespread view that hybridization between these species is unlikely seems to be mainly based on the observation that females of *C. montanus* show a strong assortative mate choice (Weih 1951; Reynolds 1980). Indeed, asymmetric types of reproductive interference seem to be a rule rather than an exception as two species are unlikely to be indiscriminate to exactly the same degree (Wirtz 1999; Gröning and Hochkirch 2008). Furthermore, species are likely to differ in several reproductive and ecological traits, such as reproductive periods and capacities, abundance and dispersion, ecological specialization, and response to environmental fluctuations that further skew the outcome of reproductive interference in the field (Gröning and Hochkirch 2008). Asymmetric hybridization has also been reported from the hybrid zone of *C. parallelus* and *C. parallelus erythropus* (Bella et al. 1992). Our results indicate a strong potential for hybridization and introgression between *C. parallelus* and *C. montanus* in nature. Indeed, individuals with intermediate morphological traits have been found in nature (Reynolds 1980), but genetic studies are missing so far. Based on the asymmetric pattern, introgression of *C. parallelus* mitochondrial haplotypes into the population of *C. montanus* is more likely than the reverse process. Given that these patterns are transferable to the natural situation, the choosiness of female *C. montanus* might prevent *C. parallelus* from colonizing the area occupied by *C. montanus*, creating a sexual barrier. At the local range boundary, *C. parallelus* females would have a higher probability to choose a wrong partner and, therefore, would be continuously outbred. This would lead to a dilution of their genetic information. On the other hand, *C. montanus*

females would only choose a conspecific partner and therefore have a higher chance to avoid outbreeding. *C. montanus* males have the chance to mate with females of both species, while *C. parallelus* males would only find conspecific mates. The low reliability of the female SMRS in *C. parallelus* might thus lead to continuous gene flow into the *C. parallelus* population. However, as *C. montanus* has a narrower ecological niche, its survival probability will only be high in wetland areas.

#### Consequences for coexistence

Of course, it remains unknown whether hybridization is the main determinant of the observed pattern of local parapatry. As *C. montanus* is a habitat specialist and *C. parallelus* is a habitat generalist, one might also suggest that ecological factors contribute to this pattern. However, our analyses of the soil moisture, vegetation, and habitat management do not support such hypotheses (unpublished data). While the *C. parallelus* populations in the north of our study area are found in drier habitats which might not be suitable for *C. montanus*, the central area of the bog should provide habitat for each the two species. Another alternative hypothesis to reproductive interference is resource competition. However, it is also unlikely that resource competition affects these two species because it is unlikely that food (grasses) or oviposition sites (soil) are limited. Habitat management (mowing) and the weather conditions seem to be much stronger determinants of population growth. In fact, the identification of a limited resource is often difficult in herbivorous insects (Strong et al. 1984).

The two grasshopper species are generally regarded as a sympatric species pair and indeed the ranges of the two species overlap significantly (Tregenza et al. 2000b). Our data suggest that this is not necessarily true on a local scale, but on the other hand, we also found sites in northern Germany where these species co-occur. We performed sweep-netting at 16 sites with known occurrence of *C. montanus* and found both species on seven of them, but only at one site these species co-occurred in similar high abundance. In the majority of cases, one species made up more than 90% of the combined catch (unpublished data). On other sites, we found very small-scaled patterns of local parapatry, with *C. montanus* occupying ca. 1,000 m<sup>2</sup> in the moist center of a site and *C. parallelus* occurring at the drier margins. These examples illustrate that each syntopic population of a species has its own history. In some cases, co-occurrence might be confined to narrow tension zones (as in our case; Fig. 1), while on other sites, these two species might co-occur over larger areas. Sometimes, the abundance of one species might be so low that the heterospecific encounter rate is much higher than the conspecific encounter rate. Furthermore, each population

might have come in contact with heterospecifics at a different time. These differences are likely to influence the evolution of assortative mating and illustrate that knowledge on the special history of each population might be necessary for final conclusions.

## Conclusions

Our results suggest that species recognition in grasshoppers is not as reliable as often concluded based on the specific song patterns. At a short distance, other factors might be more important, and erroneous mate choice seems to be more common than often assumed. The belief that songs serve as a reliable premating barrier might have caused our deficiency of knowledge concerning the ecology of hybridization. There is meanwhile accumulating evidence that hybridization is a common phenomenon in nature (Mallet 2008), affecting also the coexistence of species (Gröning and Hochkirch 2008). A better understanding of natural hybridization dynamics might provide new insights into the processes that influence species coexistence and ecological diversification. A second important result of our study is that hybridization influences also species that occur sympatrically in large parts of their ranges. For a long time, hybridization has mainly been studied in zones of secondary contact of closely related species. Our results show that sexual interactions should more often be studied in sympatric species pairs. The full Orthoptera community (or the full acoustic environment) must be taken into consideration when studying reproductive character displacement.

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