

ORIGINAL ARTICLE

Niche overlap in allotopic and syntopic populations of sexually interacting ground-hopper species

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Abstract There is accumulating evidence that sexual interactions among species (reproductive interference) could have dramatic effects for species' coexistence. It has been shown that the fitness of individuals can be substantially reduced as a consequence of reproductive interference. This might subsequently lead to displacement of a species (sexual exclusion). On the other hand, some evolutionary and ecological mechanisms might enable species to coexist, such as the divergence of mate recognition systems (reproductive character displacement), habitat partitioning, clumped dispersion patterns or different colonization capabilities. We have previously shown that the two ground-hopper species *Tetrix subulata* and *Tetrix ceperoi* interact sexually in the laboratory as well as in the field. At sites where both species co-occur niche overlap was high, suggesting that coexistence is maintained by different niche breadths rather than by habitat partitioning. To test the hypothesis that habitat partitioning does not contribute to species' coexistence, we examined whether allotopic and syntopic populations of these two species differ in niche overlap (competitive release). Our results show that niche overlap is higher in syntopic than in allotopic populations, suggesting that the site-specific habitat structure (heterogeneity) has a stronger influence on microhabitat utilization than the presence of heterospecifics. Hence, our data do not support the hypothesis that habitat partitioning plays a substantial role for the coexistence of these sexually interacting species.

Key words coexistence, competition, niche breadth, niche partitioning, reproductive interference

Introduction

Competition is frequently discussed as a factor shaping biotic communities (Gause, 1934; Schoener, 1974; Connell, 1983), although its significance is still debated (Strong, 1983; Denno *et al.*, 1995; Friggens & Brown, 2005; Kaplan & Denno, 2007). In most herbivorous insects, the identification of a shared limited resource which species may compete for remains difficult (Strong

et al., 1984). Therefore, it has been proposed that direct negative interactions (interference competition, Birch 1957) might be more important for species' coexistence than resource competition (Amarasekare, 2002). Reproductive interference (sexual interactions between species) seems to be an exceptionally powerful type of interspecific relationship, which might even lead to the displacement ("sexual exclusion") of a species (Ribeiro & Spielman, 1986; Kuno, 1992; Liou & Price, 1994; Hochkirch *et al.*, 2007a; Liu *et al.*, 2007; Hochkirch & Lemke, 2011). Reproductive interference is defined as any kind of interspecific interaction during the process of mate acquisition which adversely affects the fitness of at least one of the species involved and is caused by incomplete species recognition systems (Gröning & Hochkirch, 2008). Costly

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heterospecific interactions are principally possible during all stages of mating, including signal jamming during mate attraction, interspecific rivalry, misdirected courtship, erroneous female choice, interspecific mating attempts, interspecific mating and hybridization (reviewed in Gröning & Hochkirch, 2008). All of these types of sexual interactions may be associated with fitness costs, regardless of the fertilization of eggs. These costs can be dramatic, including not only a wastage of time and gametes, but also a decreased reproductive success or even survival of individuals (Ribeiro & Spielman, 1986). Similar to resource competition, reproductive interference is density-dependent and in most cases asymmetric. It can affect population dynamics, habitat choice and distribution of species (Gröning & Hochkirch, 2008).

Unravelling the mechanisms that promote species' coexistence in species remains a major task in ecological research (Chesson, 2000; Amarasekare, 2003; Morris, 2003; Agrawal *et al.*, 2007) and the same is true for species engaged in interspecific sexual interactions (Gröning & Hochkirch, 2008). While the mechanisms of coexistence have frequently been studied in the context of resource competition, such studies are still sparse in the context of reproductive interference (but see Gröning *et al.*, 2007b). Different from species competing for shared resources, species involved in sexual interactions might increase their fitness mainly by avoiding direct interactions and not by partitioning other niche dimensions, such as food or oviposition sites. The mechanisms which may enable sexually interacting species to coexist include ecological mechanisms, such as spatial, temporal or habitat partitioning (e.g. Singer, 1990), dilution effects from clumped dispersion patterns (e.g. Gröning *et al.*, 2007b) or local abundance (e.g. Söderbäck, 1994), different colonization capabilities or population dynamics (Westman *et al.*, 2002) and evolutionary mechanisms, that is, reproductive character displacement (Brown & Wilson, 1956). While the ecological mechanisms act by decreasing the frequency of heterospecific encounters, the latter represents an evolutionary adaptation to reduce the costs of reproductive interference. Habitat partitioning is one of the most important mechanisms promoting species' coexistence (Morris, 2003) and has also been reported from sexually interacting species (Kawano, 2004). A phenomenon which is strongly associated with niche partitioning is competitive release. If niche partitioning is caused by ongoing interactions, competitive release should occur in the absence of a competitor (Larsen, 1986). Although reproductive interference differs from competition by the absence of a shared limited resource (Gröning & Hochkirch, 2008), it is reasonable to suggest that release from sexual interactions should be associated with a similar pattern.

If niche overlap is lower at sites where both species occur (syntopic occurrence *sensu* Rivas, 1964) than at sites where a species is missing (allotopic occurrence), habitat partitioning is unlikely to be a consequence of ongoing competition or reproductive interference as habitat utilization could be influenced by environment factors (e.g., microhabitat composition) of the location. Therefore, researchers should investigate not only habitat utilization of the organisms but also environmental factors of study sites.

The two ground-hopper species *Tetrix ceperoi* (Bolívar, 1887) and *T. subulata* (Linnaeus, 1758) occur sympatrically in large parts of Europe, but rarely co-occur at the same site (Farrow, 1963; Kleukers *et al.*, 1997; Gröning *et al.*, 2005). Resource competition is unlikely in these polyphagous species, as food (algae, microorganisms, mosses) is abundant in their habitats and the oviposition site (soil) is also not limited. However, we have previously shown that these two species engage in sexual interactions in the laboratory as well as in the field (Gröning *et al.*, 2007b; Hochkirch *et al.*, 2007a) and also with other species (Hochkirch *et al.*, 2008a). Under experimental conditions the mating frequency and reproductive success of *T. ceperoi* decreased in the presence of *T. subulata*, while in the field males of both species were equally indiscriminate in their mate choice (although heterospecific mating rarely occurs and the species do not hybridize). An analysis of microhabitat utilization and dispersion patterns at a site where both species co-occur suggests that their coexistence is promoted by different niche breadths rather than by habitat partitioning (Gröning *et al.*, 2007b), that is, the means associated with different habitat parameters are rather similar, but their variances are not. Both species preferred damp, open patches with a warm microclimate, but *T. ceperoi* had a stronger preference for bare ground than *T. subulata*. Due to its broader niche, the dispersion of *T. subulata* was less aggregated than that of *T. ceperoi*. Hence, the frequency of heterospecific encounters was reduced for *T. ceperoi* at patches with a high intraspecific density and for *T. subulata* at patches where *T. ceperoi* was absent (Gröning *et al.*, 2007b). However, if niche overlap was higher in allotopic populations than in the syntopic population, habitat partitioning might still play a role for coexistence. Here, we test this hypothesis by comparing niche overlap and niche breadth at sites where only one of the two *Tetrix* species exists ("allotopic populations") with the syntopic populations. We propose that release from reproductive interference should lead to an increased niche overlap of allotopic populations compared with the syntopic populations, as has been shown in allopatric congeneric tropical grasshopper species (Hochkirch, 2001, 2010). A similar niche overlap

in syntopic populations as in allotopic populations would imply that microhabitat utilization is not affected by reproductive interference, whereas a higher niche overlap in syntopic than between allotopic populations would suggest that habitat use is strongly influenced by the specific vegetation structure or the climatic situation of the sites or years. In these two latter cases, other mechanisms might promote species coexistence.

Materials and methods

The study objects

Ground-hoppers (Tetrigidae) are a basal group of Orthoptera which mainly occur in damp, open habitats (Paranjape *et al.*, 1987; Hochkirch *et al.*, 2008b). *T. ceperoi* is distributed in the Mediterranean and Western Europe, whereas *T. subulata* has a Holarctic distribution. The area of overlap comprises northern Spain, France, southern England, Central Europe, Italy and the Balkans (Kleukers *et al.*, 1997). Both species are terricolous and associated with damp, open habitats, but *T. subulata* is generally more widespread and also occurs in wet grasslands (Farrow, 1963; Detzel, 1998; Gröning *et al.*, 2005). *T. ceperoi* has been found in similar habitat types in areas where *T. subulata* is rare or missing, such as the German Wadden Sea Islands (Gröning *et al.*, 2005). Tetrigidae feed on a variety of algae, mosses, small plants and detritus (Hochkirch *et al.*, 2000). Adults of both species reproduce in May and June (Kleukers *et al.*, 1997) and utilise visual and vibrational signals for mate recognition (Hochkirch *et al.*, 2006; Kocarek, 2010). Although the species show remarkable differences in their courtship displays, heterospecific mating has been observed in the laboratory (Hochkirch *et al.*, 2007a) and males of both species are indiscriminate in their mate choice in the field (Gröning *et al.*, 2007b). In all Tetrigidae sexual size dimorphism is distinct (Hochkirch & Gröning, 2008): Females are substantially larger than males as they pass through one additional nymphal instar (Ingrisch & Köhler, 1998). Males of both species exhibit a stronger preference for bare ground than females, possibly due to the greater energetic requirements of the females (Forsman & Appelqvist, 1999; Hochkirch *et al.*, 2007b). Females of both species oviposit in moist soil. Both sexes of *T. ceperoi* are smaller than the corresponding sex in *T. subulata* (Kleukers *et al.*, 1997).

The study sites

We collected data on the microhabitat preferences on five sites at a restored floodplain of the river Hase which

hosts populations of both species (Gröning *et al.*, 2007b) and on eight sites on the isle of Langeoog, where only *T. ceperoi* occurs (Gröning *et al.*, 2007a; Hochkirch *et al.*, 2007b). Moreover, we used data which were collected in 1998 and 1999 at a pond in the city of Bremen, where *T. subulata* and *Tetrix tenuicornis* occur (Hochkirch *et al.*, 1999; Hochkirch *et al.*, 2000). The maximum distance between these sites is 120 km. The syntopic populations (Hase) occur near the town of Haselünne (Emsland, Germany), and represent one of the few areas in north-western Germany where both species coexist in high abundance. Due to restoration measures in the winter of 2001/2002 (Exeler *et al.*, 2009), a mosaic of ephemeral ponds, moist swales and inland sand dunes has been created (Gröning *et al.*, 2007b). The area (37 ha) is characterized by high dynamics due to winter flooding and is managed by extensive cattle grazing. *T. ceperoi* and *T. subulata* have been recorded from the sites since 2004 (Gröning *et al.*, 2005). They co-occur in high numbers in moist hollows, ditches and along the open shore of ephemeral ponds, five sites of which have been chosen for data collection. The sites on the isle of Langeoog (allotopy: *T. ceperoi*) are moist dune slacks, ephemeral ponds, fens, grasslands and the transitional zone between dunes and salt marshes (Gröning *et al.*, 2007a). The isle of Langeoog is a young dune island in the German Wadden Sea with a size of 20 km². It belongs to the East Frisian Islands and is protected as part of the national park “Niedersächsisches Wattenmeer”. *T. ceperoi* was recorded from 19 sites on this island (Gröning *et al.*, 2005), eight of which were chosen for data collection (Gröning *et al.*, 2007a; Hochkirch *et al.*, 2007b). Other Tetrigidae (potential competitors) are virtually missing on Langeoog and were absent from all of our study sites (Gröning *et al.*, 2007a). Initially, we intended to study release effects only for *T. ceperoi*, but as data for *T. subulata* was available from a previous study (albeit only from one site), we also included these in our analyses. The pond in the city of Bremen (allotopy: *T. subulata*) is located on a sand deposition site (“Niederbührener Sandfeld”) in the floodplain of the river Weser, which was created during the extension of the closely situated river (Hochkirch *et al.*, 1999; Hochkirch *et al.*, 2000). At this site another *Tetrix* species (*T. tenuicornis*) occurred, which is xerophilous and unlikely to interact with *T. subulata* (Hochkirch *et al.*, 1999).

Data collection

To compare the microhabitat utilization of syntopic and allotopic populations of both species, we used the method

described by Gröning *et al.* (2007a) and Hochkirch *et al.* (2008c). This method focuses on measuring habitat utilization by individuals in order to obtain data on microhabitats rather than data on correlations between population size and habitat factors. Based on this data it is possible to identify means and variances for each habitat parameter in a given population. The syntopic populations (Hase) were studied from May 3 to June 28, 2006 (Gröning *et al.*, 2007b). The field work for the allotopic populations of *T. ceperoi* (Langeoog) was carried out from May 7 to June 26, 2004 (see details in Gröning *et al.*, 2007a; Hochkirch *et al.*, 2007b). Data for the allotopic population of *T. subulata* (Bremen) was collected during two studies on the microhabitat preferences, foraging behavior and escape behavior of *T. subulata* from May 27 to June 17, 1998 and from May 18 to June 15, 1999 (Hochkirch *et al.*, 1999; Hochkirch *et al.*, 2000; Hochkirch *et al.*, 2002). The collected data differed slightly between the studies due to the different research objectives. Vegetation structure and microclimate are known to be the most important determinants of Orthoptera occurrence (Ingrisch & Köhler, 1998; Hochkirch & Adorf, 2007). We only included vegetation parameters which were recorded in the majority of the studies. Microclimatic data were excluded as these strongly depend on weather conditions. All data were obtained at the exact location of undisturbed individuals. For each ground-hopper, we noted species, sex, behavior, time and date, as well as the substrate on which the insects perched (including the categories bare ground, litter, grasses, forbs and mosses). In a circle of 30 cm diameter surrounding the focal insect, we recorded the maximum vegetation height and estimated the vegetation cover, including the relative frequencies of bare ground, litter, grasses, forbs and mosses. At the Hase and Langeoog sites, a corresponding control sample was taken in 1-m distances in a random direction (Gröning *et al.*, 2007a; Gröning *et al.*, 2007b). Such a control sample was not recorded at the Bremen site (as these data were originally collected for another research project). In total, 230 syntopic records were available for each species, 521 allotopic records for *T. subulata* and 412 allotopic records for *T. ceperoi*. During some years, single parameters were not recorded. In 1998, data on the cover of litter was not recorded at the allotopic population of *T. subulata* (but in 1999). Vegetation height was not recorded in Bremen in 1999 (but in 1998).

Statistical analyses

To compare the microhabitat utilization (habitat partitioning) of *T. ceperoi* and *T. subulata* in syntopic and

allotopic populations, we performed two-way analyses of variance (ANOVAs) for metric data (vegetation cover, vegetation height). Since we obtained individual data sets rather than abundance data, we used “population type” (i.e., allotopic or syntopic) and “species” as explanatory variables and the measured parameters as response variables. If necessary, data were Box-Cox-transformed using Venables and Ripley’s MASS library for R (Venables & Ripley, 2002), which reveals the optimal power transformation (λ) to fit the data to meet the model assumptions. We used χ^2 cross table tests to analyze substrate data. Tests for differences between the locations of the insects and the corresponding control samples (paired *t*-tests) have been published elsewhere (Gröning *et al.*, 2007a; Gröning *et al.*, 2007b). To test for different niche breadths between syntopic and allotopic populations, the variances associated with the means of the insect’s location were analyzed with Fisher’s *F*-test. We used the same analyses (ANOVA and Fisher’s *F*-test) to test for differences in the habitat structure (control samples) between the syntopic populations and the allotopic populations of *T. ceperoi*. The analyses were carried out in R 2.12.0 (R Development Core Team, 2007). All errors provided in parentheses or as error bars are standard errors.

We performed a standardized principal component analysis (PCA) in order to identify correlations between the environmental factors (i.e., vegetation structure). We had to exclude one of the allotopic data sets (1999) for *T. subulata* and one vegetational parameter (cover of litter), as not all variables were recorded in every year. Due to the variable scales of our data set (cm, % cover) we used the function “rda” of the community ecology package vegan 1.8–8 for R (Oksanen *et al.*, 2007) to scale the factors by their proportional eigenvalues. The locations of *T. ceperoi* and *T. subulata* were fitted as vectors onto the ordination using the function “envfit” for R. This method also generates an r^2 measure and significance values based on the probability that random permutations would yield a higher degree of fit than the true data (Oksanen *et al.*, 2007).

We chose the Czechanowski index (Gotelli & Entsminger, 2001) to quantify niche overlap between *T. ceperoi* and *T. subulata* at allotopic and syntopic populations for all microhabitat parameters. The Czechanowski index ranges from 0 (no shared resource states) to 1 (identical habit utilization). To test whether the observed niche overlap differed from a random pattern, we carried out null model analyses with EcoSim 7.0 (Gotelli & Entsminger, 2001). EcoSim simulates patterns of niche overlap and compares these randomized results with the observed data matrix. We used the algorithm RA3 (Winemiller & Pianka, 1990) to test for non-random niche overlap. In this

Table 1 Results of the two-way ANOVAs, using species (*Tetrix ceperoi* vs. *T. subulata*) and population type (allotopic vs. syntopic) as explanatory variables and vegetation parameters as response variables.

Parameter	Species		Population type		Species : population type	
Vegetation height	$F_{1,1053} = 11.5$	$P < 0.001$	$F_{1,1053} = 5.41$	$P = 0.020$	$F_{1,1053} = 0.07$	$P > 0.050$
Cover of bare ground	$F_{1,1388} = 42.2$	$P < 0.001$	$F_{1,1388} = 30.4$	$P < 0.001$	$F_{1,1388} = 2.92$	$P > 0.050$
Cover of grasses	$F_{1,1388} = 53.5$	$P < 0.001$	$F_{1,1388} = 1.49$	$P > 0.050$	$F_{1,1388} = 8.79$	$P = 0.003$
Cover of litter	$F_{1,1202} = 1.65$	$P > 0.050$	$F_{1,1202} = 4.96$	$P = 0.026$	$F_{1,1202} = 11.7$	$P < 0.001$
Cover of forbs	$F_{1,1388} = 13.2$	$P < 0.001$	$F_{1,1388} = 3.95$	$P = 0.047$	$F_{1,1388} = 4.89$	$P = 0.027$
Cover of mosses	$F_{1,1388} = 48.9$	$P < 0.001$	$F_{1,1388} = 28.2$	$P < 0.001$	$F_{1,1388} = 24.9$	$P < 0.001$

procedure, the observed niche breadth of each species is retained, but the utilization of any resource state is allowed, including categories that were available but not used by the species. For each data set 10 000 replicates were created in the simulation.

Results

Microhabitat utilization

Tetrix ceperoi and *T. subulata* differed significantly in microhabitat utilization with respect to vegetation height

and the cover of bare ground, grasses, forbs and mosses (Table 1). Although the general pattern was similar among syntopic and allotopic populations (except for litter), the differences were generally smaller in the syntopic populations (Fig. 1). The vegetation was higher at the locations of *T. subulata* (24.0 cm \pm 0.97) than at the locations of *T. ceperoi* (20.4 cm \pm 0.60), but in both species vegetation height was greater in the allotopic populations than in the syntopic populations (Fig. 1). Cover of bare ground was greater at the locations of *T. ceperoi* (43.1% \pm 1.27%) than at the locations of *T. subulata* (32.2% \pm 1.12%). Again, no interaction occurred between the factors “species” and “population type”, as both species utilized fewer open

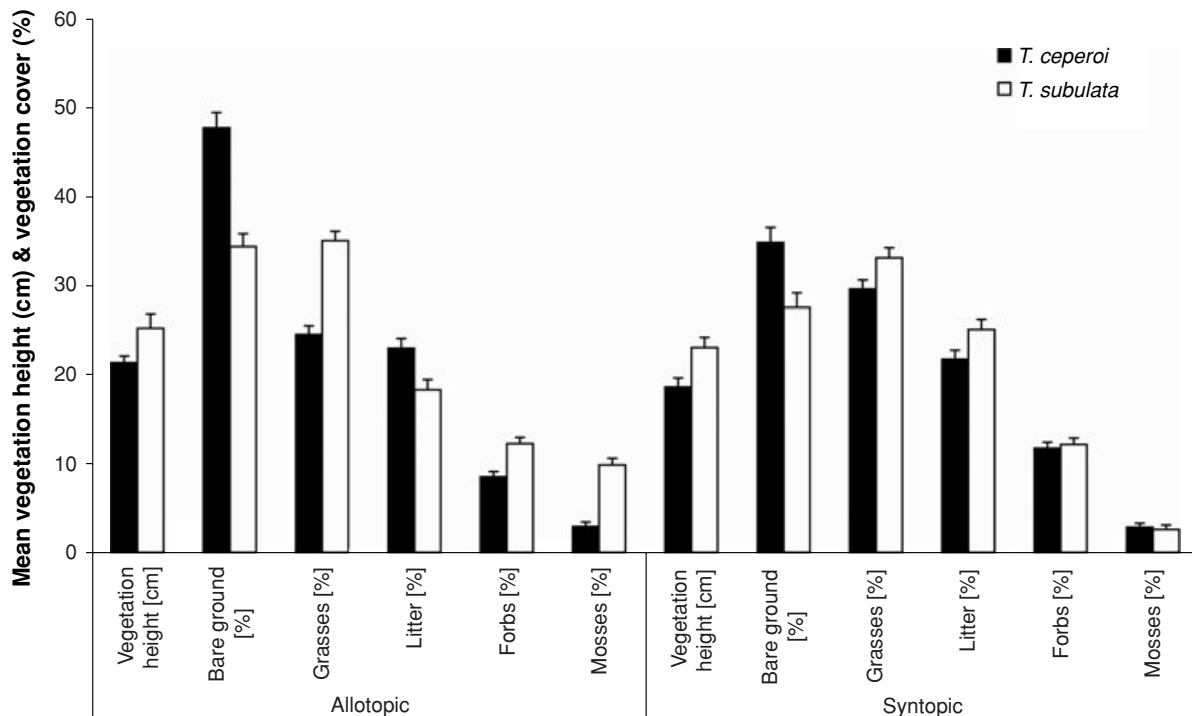


Fig. 1 Average cover of vegetation parameters and maximum vegetation height in a circle of 30 cm surrounding the location of *Tetrix ceperoi* and *T. subulata* at allotopic and syntopic locations. Error bars are standard errors. Note that the differences of allotopic populations are greater than the differences between syntopic populations.

Table 2 Results of Fisher's *F*-tests for differences in the variance of the location of both ground-hopper species in syntopic and allotopic populations.

Factor	<i>T. ceperoi</i>				<i>T. subulata</i>			
	V_{Syn}	V_{Allo}	<i>F</i>	<i>P</i>	V_{Syn}	V_{Allo}	<i>F</i>	<i>P</i>
Vegetation height	237.09	221.04	0.93	0.540	310.24	484.11	1.56	0.001
Cover of bare ground	650.83	1185.79	1.82	<0.001	615.01	1080.04	1.76	<0.001
Cover of grasses	232.65	401.08	1.72	<0.001	295.48	581.89	1.97	<0.001
Cover of litter	240.16	478.80	1.99	<0.001	292.90	444.12	1.52	<0.001
Cover of forbs	111.09	138.00	1.24	0.068	119.46	247.20	2.07	<0.001
Cover of mosses	46.33	104.01	2.25	<0.001	56.48	290.13	5.14	<0.001

Denominator *df* = 229; *Tetrix ceperoi*: numerator *df* = 411, *T. subulata*: numerator *df* = 519, *T. subulata* (vegetation height): numerator *df* = 183, *T. subulata* (litter): numerator *df* = 333. Note that in all significant cases V_{Syn} (variance in the syntopic populations) is smaller than V_{Allo} (variance in the allotopic populations).

patches in the syntopic populations (Fig. 1). The cover of litter was generally greater in syntopic populations ($23.4\% \pm 0.76\%$) than in allotopic populations ($20.8\% \pm 0.79\%$), but in the syntopic population *T. subulata* utilized litter more often than *T. ceperoi*, whereas the reverse pattern was found in allotopic populations (Table 1, Fig. 1). *T. subulata* was more often found at localities with a higher percentage of grasses ($34.4\% \pm 0.81\%$), forbs ($12.2\% \pm 0.53\%$) and mosses ($7.6\% \pm 0.55\%$) than *T. ceperoi* (grasses, $26.3\% \pm 0.73\%$; forbs, $9.6\% \pm 0.45\%$; mosses, $2.9\% \pm 0.36\%$), but this difference was smaller in the syntopic population (Table 1, Fig. 1). In both species, the relative frequencies of substrate types on which the insects perched differed significantly between the population types. *T. ceperoi* was found more often on grasses and less often on mosses in the syntopic than in the allotopic populations (χ^2 cross table test, $\chi^2_4 = 57.64$, $P < 0.001$). *T. subulata* perched more often on litter in the syntopic populations and less often on mosses and grasses than in the allotopic population (χ^2 cross table test, $\chi^2_4 = 47.08$, $P < 0.001$).

Niche breadth

To estimate differences in niche breadth, we compared the variances of each parameter between the populations (Gröning *et al.*, 2007b). For *T. subulata*, niche breadth was significantly narrower in the syntopic population than in the allotopic population as the variance for all factors was greater at the latter (Table 2). A similar pattern was found for *T. ceperoi*, except for the parameters "vegetation height" and "cover of forbs", which did not differ significantly between syntopic and allotopic populations.

Niche overlap

The niche overlap of syntopic populations of *T. ceperoi* and *T. subulata* was generally higher than the niche overlap of allotopic populations (Fig. 2, Table 3). The Czechanowski index varied between 71.5% and 79.9% for the allotopic populations and between 78.7% and 97.4% for syntopic populations. In the syntopic populations, the observed niche overlap was significantly higher

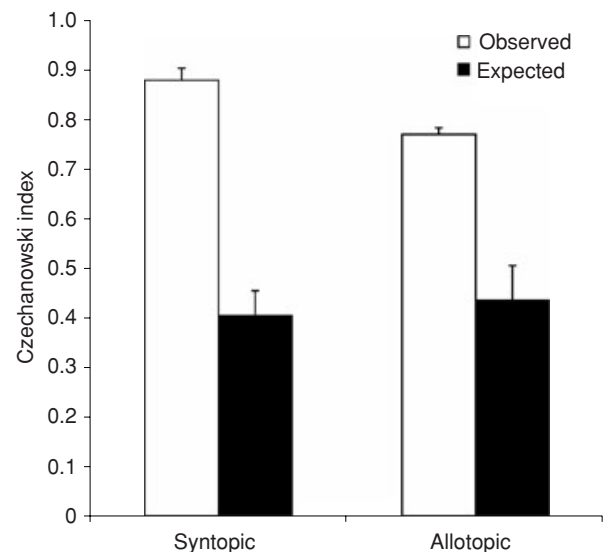


Fig. 2 Average observed and expected niche overlap between *Tetrix ceperoi* and *T. subulata* for syntopic and allotopic populations, calculated with EcoSim 7.0. For each data set 10 000 replicates were created in the simulation. Note that the observed niche overlap was higher for the syntopic populations than for the allotopic populations.

Table 3 Observed and expected mean niche overlap (Czechanowski index) of *Tetrix ceperoi* and *T. subulata* for allotopic and syntopic populations, calculated with EcoSim 7.0.

	Allotopic			Syntopic		
	Obs.	Exp.	<i>P</i> obs. > Exp.	Obs.	Exp.	<i>P</i> obs. > Exp.
Substrate	0.791	0.511	0.063	0.787	0.452	0.041
Vegetation height	0.799	0.394	<0.001	0.843	0.318	<0.001
Bare ground	0.753	0.741	0.367	0.822	0.586	<0.001
Mosses	0.792	0.172	<0.001	0.917	0.207	<0.001
Grasses	0.733	0.523	0.004	0.891	0.544	<0.001
Forbs	0.715	0.260	<0.007	0.974	0.320	<0.001
Litter	0.799	0.436	0.003	0.909	0.395	<0.001

For each data set 10 000 replicates were created in the simulation. Obs, observed; Exp, expected.

than expected by chance for all habitat descriptors. The same was true for the allotopic populations, except for the parameters “bare ground” and “substrate”, for which the niche overlap between *T. ceperoi* and *T. subulata* did not differ from a random pattern.

Multivariate analysis

A plot of the first two principal components (explaining 56.8% of the total variance) is shown in Figure 3, including the vectors of the insects' locations and the control samples. In this multidimensional framework there was a positive correlation between locations of *T. ceperoi* and the factor “bare ground”. This association was stronger for the allotopic populations ($r^2 = 0.085$, $P < 0.001$) than for the syntopic populations ($r^2 = 0.007$, $P < 0.001$). The allotopic populations of *T. subulata* were negatively correlated with vegetation height and grass cover ($r^2 = 0.012$, $P < 0.001$), but the syntopic populations had no significant correlation with the vegetation matrix ($r^2 = 0.003$, $P = 0.073$). The control samples of the syntopic populations were positively correlated with vegetation height and grass cover ($r^2 = 0.016$, $P < 0.001$), whereas the control samples of the allotopic populations of *T. ceperoi* (Langeoog) correlated negatively with the cover of bare ground ($r^2 = 0.041$, $P < 0.001$). The difference between the loadings (i.e., vectors) of both species was smaller in the syntopic populations than in the allotopic populations.

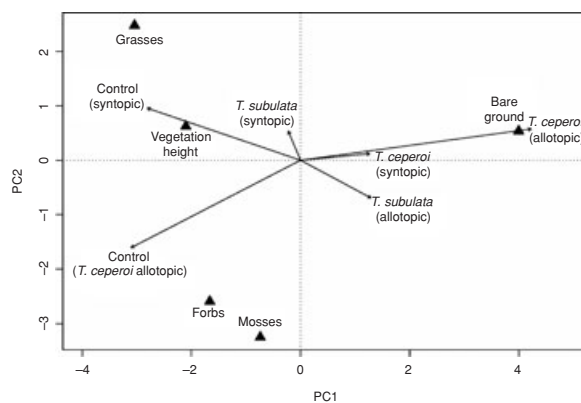


Fig. 3 Plot of the first two principal components of a standardized principal components analysis of the environmental parameters (explaining 56.8% of the total variance). The factors were standardized to unit variance using correlation coefficients to achieve a more balanced ordination. Triangles are factor loadings. The locations of *Tetrix ceperoi* and *T. subulata* as well as the control samples were fitted as vectors onto the ordination. There was no significant correlation for *T. subulata* (syntopic) with the environmental parameters. No control samples were available for *T. subulata* (allotopic).

Control samples

To test for general differences in the habitat structure between the syntopic populations and the allotopic populations of *T. ceperoi*, we compared the control samples using ANOVAs and Fisher's *F*-tests (Table 4). The analyses revealed that the cover of litter, forbs and mosses was significantly greater at the allotopic populations than at the syntopic ones. More importantly, nearly all parameters had a greater variance in the allotopic population of *T. ceperoi* than in the syntopic populations, suggesting that habitat heterogeneity was greater in the allotopic populations. “Niche overlap” of the control samples between the allotopic and syntopic populations was higher than expected for all measured variables (Table 4). The Czechanowski indices varied between 71.8% and 86.3% and nearly all were lower than the values for *T. ceperoi* and *T. subulata* in the syntopic populations. Regarding the parameter “cover of bare ground”, niche overlap was even higher between the allotopic populations of both species than between the control samples for *T. ceperoi*.

Discussion

Our analysis revealed that the niche overlap in syntopic populations of the two *Tetrix* species was higher than the niche overlap of allotopic populations. These results

Table 4 Results of ANOVAs (df: 1 852), Fisher's *F*-tests and niche overlap analyses to test for differences in the habitat structure of the control samples taken in the syntopic populations and the allotopic populations of *Tetrix ceperoi*.

Parameter	ANOVA		Fisher's <i>F</i> test				Niche overlap		
	<i>F</i>	<i>P</i>	V_{Syn}	V_{Allo}	<i>F</i>	<i>P</i>	Obs.	Exp.	<i>P</i>
Vegetation height	0.08	> 0.050	442.52	382.81	0.87	> 0.05	0.863	0.437	<0.001
Cover of bare ground	0.21	> 0.050	565.76	955.50	1.69	< 0.001	0.718	0.452	0.012
Cover of grasses	0.07	> 0.050	384.83	777.80	2.02	< 0.001	0.849	0.157	0.003
Cover of litter	11.30	< 0.001	322.51	654.15	2.03	< 0.001	0.748	0.595	0.005
Cover of forbs	15.30	< 0.001	196.09	344.12	1.75	< 0.001	0.797	0.379	<0.001
Cover of mosses	14.10	< 0.001	62.64	336.02	5.36	< 0.001	0.826	0.511	0.008

Observed and expected mean niche overlap were calculated with EcoSim 7.0 (obs.: observed Czechanowski index; exp.: expected Czechanowski index). For each data set 10 000 replicates were created in the simulation (*P* is only given for obs. > exp.).

do not support the hypothesis that habitat partitioning plays a fundamental role for maintaining coexistence in these two species as no competitive release was found. It might be argued that only few aspects of the niche (habitat structure) have been analyzed and some parameters (e.g., diet, phenology, microclimate) have not been measured. However, release from sexual interactions is mainly possible by reducing the number of heterospecific encounters (Gröning *et al.*, 2007b). The encounter rate is determined by time (e.g. phenology, daily activity pattern) and space (habitat utilization, dispersion). A shift in microclimatic preferences or diet would only be an effective means to reduce the costs associated with reproductive interference, if this would alter microhabitat utilization (which we measured in this study). Moreover, most Orthoptera are polyphagous and their diet is mainly determined by the size of their mandibles (Chapman, 1990). This is particularly true for these small species. Both species feed on a variety of algae, mosses, detritus and sprouts of forbs and grasses (Hochkirch *et al.*, 2000; Gröning *et al.*, 2007a). It has been suggested that males of *T. subulata* might not be able to bite through leaves of grasses or forbs due to their smaller body size compared to females (Hochkirch *et al.*, 2000). Thus, intraspecific (intersexual) differences in diet are greater and more important than the interspecific difference. Indeed, the sexes of both species differ in microhabitat utilization (Forsman & Appelqvist, 1999; Hochkirch *et al.*, 2007b), but the intersexual difference was similar in both species (males had a stronger preference for bare ground) and this seems to be mainly caused by differential energetic requirements of the sexes due to different costs of reproduction (Hochkirch *et al.*, 2007b). Interestingly, this sexual difference was not found in the syntopic population at the Hase, which might be explained

by a less heterogeneous habitat structure (but also by the lower sample size).

Temporal niche partitioning is another suitable mechanism to reduce the rate of heterospecific encounters (Armstrong & McGehee, 1980; Chesson, 2000; Albrecht & Gotelli, 2001), but *T. subulata* and *T. ceperoi* have a similar daily activity pattern (Koen, 1996). Both species are diurnal and active mainly during warm weather conditions. Behavioral observations in the syntopic populations showed that heterospecific encounters (and mating attempts) occur throughout the day (Gröning *et al.*, 2007b). Moreover, the phenologies of both species substantially overlap (Kleukers *et al.*, 1997). Grid mapping in one of the syntopic populations revealed that the phenological niche overlap was 93.1% in 2005 and 76.3% in 2006 (Gröning *et al.*, 2007b). These results show that niche partitioning is unlikely to play a role for coexistence in these two species.

Previous analyses suggest that the dispersion patterns of the two ground-hopper species are more important for reducing the frequency of heterospecific encounters in syntopic populations than habitat partitioning (Gröning *et al.*, 2007b). The dispersion of these insects seems to be strongly determined by their niche breadth and the structure of the available habitat. *T. ceperoi* has a narrower niche and a more aggregated dispersion than *T. subulata* in the syntopic populations. Although our analyses show that the syntopic populations of both species have narrower niches than the allotopic populations, niche overlap was higher in the syntopic populations. Hence, the specific habitat structure of the sites seems to be of major importance for the observed pattern. Our analyses of the control samples of *T. ceperoi* show that habitat heterogeneity (i.e., variance) was lower in the syntopic populations

than in the allotopic ones, leading to an increased niche overlap at the syntopic localities. Unfortunately, no control measures were taken for the allotopic population of *T. subulata*, but the greater variance at the insects' locations (Table 2) suggests that a similar pattern might be found at the site in Bremen. Moreover, the different weather conditions during the study years might affect microhabitat utilization in both species. However, it should be noted that we only obtained data on sunny days when the insects are usually active. One might also argue that differences among sites will generally be greater than between microhabitats at a single site, but it should be noted that exactly the opposite pattern has been observed among allopatric *Afrophaeoba* species on different mountain blocks in Tanzania (Hochkirch, 2010).

It is rather surprising that the few sites in northwestern Germany which host mixed populations of both species are less heterogeneous than sites where only one species occurs. In fact, *T. ceperoi* and *T. subulata* seem to be forced to use similar microhabitat structures in the Hase floodplain and cannot reduce their niche overlap due to limited habitat heterogeneity. This might increase the frequency of reproductive interference between these species. Although our previous analyses suggest that coexistence is promoted by the different dispersion patterns even in the absence of habitat partitioning (Gröning *et al.*, 2007b), some alternative explanations remain to be studied. One question of major importance is how persistent the syntopic populations are. Both species were found for the first time at the Hase in 2004 and still co-occurred in high numbers in 2008. The narrow niche breadths of both species compared to the allotopic populations suggest that the habitat quality at the Hase is not optimal for both *Tetrix* species, particularly for *T. ceperoi*, which has even a narrower niche at the Hase. Therefore, it has been argued that *T. ceperoi* might disappear from the site due to rapid natural succession before the costs of reproductive interference will affect population dynamics (Gröning *et al.*, 2007b). The damp areas of the study site undergo a fast succession by young willows and bulrush, which might render these floodplain habitats unsuitable for *T. ceperoi*. Indeed, both *Tetrix* species are pioneer species and able to rapidly colonize new sites (Detzel, 1998). Hence, the coexistence of the populations of both species might be ephemeral and the high dispersal capabilities might promote species' coexistence in a metapopulation context (Levins, 1969; Gordon, 2000). Moreover, populations of both species are known to undergo remarkable fluctuations (Maas *et al.*, 2002). Climatic oscillations might have a strong influence on the survival of eggs and nymphs of these strategists. Such abiotic factors might be more important for population dynamics than the costs associated

with reproductive interference, but the influence of each factor will be difficult to disentangle in the field.

Habitat utilization is known to be of fundamental importance for understanding species' coexistence (Morris, 2003). Habitat partitioning is frequently discussed as a key mechanism promoting the coexistence of competing species (e.g., Werner *et al.*, 1977; Wisheu, 1998). Our results show that syntopic populations of sexually interacting species do not necessarily reduce the number of heterospecific encounters by habitat partitioning or temporal niche partitioning. Other mechanisms of segregation or dilution might be equally or even more important for species' coexistence (Gröning *et al.*, 2007b). These mechanisms include the dispersion patterns in heterogeneous habitats (Amarasekare, 2003), but also dispersal capabilities which might enable species to coexist on a metapopulation scale (Gordon, 2000). Pioneer species, such as the two *Tetrix* species, are characterized by strong colonization capabilities and high rates of population growth, both of which are of high importance for population dynamics (Sibly & Hone, 2002). The spatio-temporal dynamics of colonization, extinction and population dynamics might superimpose the effects of reproductive interference. There is a strong need for more studies on the potential mechanisms that enable sexually interacting species to coexist. Biological invasions, habitat degradation and range shifts driven by climate change alter the structure of biotic communities and could increase the number of sexual interactions among species which have been previously separated geographically or ecologically (Samways, 1977; Westman *et al.*, 2002; Liu *et al.*, 2007; Gröning & Hochkirch, 2008). As the costs associated with reproductive interference are density-dependent (Gröning & Hochkirch, 2008), future research should also include experiments on habitat utilization and niche partitioning at different intra- and interspecific densities. Such experiments might help to uncover the underlying principles of coexistence.

Acknowledgments

We are grateful to Kathrin A. Witzemberger for critical comments that helped to improve the manuscript. Günter Grein and Henrich Klugkist provided information concerning the distribution of the investigated species. The fieldwork in Bremen was done during a students' course in behavioral ecology. The participants in 1998 were Michael Folger-Rüter, Iris Gehrken, Malte Götz, Anke Gulau, Carola Harmuth, Frauke Hellwig, Andrea Intemann, Christian Keithahn, Stefan Länder, Helge Mühl, Udo Palckruhn, Melanie Papen, Andrea Peiter, Ole Rohlf, Gitta Spiecker, Stefan Vogt, Marco Zimmermann and

Marion Zimmermann. In 1999, the data were collected by Christoph Kulmann, Tamara Loos, Tede Lorenzen, Corinna Ahrensfeld, Anne Osburg, Maren Reichelt, Claudia Schlüter and Maria Vassilakaki. The fieldwork on Langeoog was carried out by Sascha Krause and Judith Kochmann. At the Hase site, Alexander Finger, Niklas Lücke, Andreas Michalik and Felix Schaefer helped to collect data. Access to the study sites was kindly permitted by the district administration Weser-Ems (National Park Administration). Financial support was provided by research grants to J. Gröning (GradFÖG, Reinhold-Tüxen-Gesellschaft e.V., Forschungspool of the University of Osnabrück) and by the Foundation of Gerhard ten Doornkaat-Kohlmann (grants to S. Krause and J. Kochmann).

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Accepted April 20, 2011