

Coexistence of two related bush-cricket species (Orthoptera: *Tettigonia caudata*, *T. viridissima*) in an agricultural landscape

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Abstract: Competition is a basic type of interaction between species. Because complete competitors cannot exist in one habitat, closely related species must show at least slight differences in their biology or ecology. In the present study, we analyzed the habitat use of the two closely related bush-cricket species *Tettigonia caudata* and *T. viridissima* which often occur syntopically. The meso- and microhabitat use of males was compared in an agricultural landscape in NE Germany. Males of both species were found to use similar mesohabitats and to prefer dense and high vegetation. Microhabitats differed significantly in two aspects: Microhabitats of *T. caudata* had a higher proportion of herbs, while *T. viridissima* used higher song posts. These differences in microhabitats might explain the co-occurrence of the bush-cricket species in open habitats. However, variation between the two species might also take place during other life-cycle stages such as during egg development.

Key words: Bush-cricket; competitive exclusion; Ensifera; habitat requirement; interspecies competition; niche concept

Introduction

Interspecies competition represents a basic interaction but one which has often given rise to controversial discussions (Kaplan & Denno 2007). Competition among species arises if two or more species require an identical but limited resource (Begon et al. 1990). Competition might lead to a reduction in growth or reproduction or even to a displacement of one of two (or more) closely related species because complete competitors cannot coexist, according to the ‘competitive exclusion principle’ (Hardin 1960). Similarly, and linked with this concept, the ‘niche theory’ (Hutchinson 1957) states that two closely related species which have identical niches (i.e. they compete for the same resources) cannot coexist in one habitat (Speight et al. 2008). Coexistence of two closely related species is therefore only possible if species show at least slight differences in their biology or ecology (Speight et al. 2008). Closely related species might be able to coexist due to spatial segregation (e.g., different nesting or oviposition sites), temporal segregation (e.g., different daily or annual activity) or differences in food preferences (e.g., foraging on different host plants). Moreover, additional factors such as parasitoids and predators might decrease the abundance of competing species relative to the carrying capacity of a habitat. In this case, competition between species does not exist because resources are not limited, and coexistence might become possible (Speight et al. 2008).

Among insects, many Orthoptera species colonize man-made habitats (Detzel 1998). In particular, the Ensifera of the genus *Tettigonia* are known to be common in agricultural landscapes, occurring in dense vegetation of fields, fallows and fringes (Detzel 1998). Agroecosystems are often characterized by high disturbance and production rates (= broad nutrient and food supply) which offer some species very suitable life conditions. In some parts of Central Europe, the three closely related species *Tettigonia caudata* (Charpentier, 1842), *T. cantans* (Fuessli, 1775) and *T. viridissima* (L., 1758) occur syntopically (Nadig 1991; Krištin et al. 2007). In large areas of Germany, *T. cantans* and *T. viridissima* are known to be vicariant species: The more eurytopic and slightly thermophilic *T. viridissima* is very common and widespread, except in regions with wet and cool climatic conditions such as the Northwest German lowland and higher mountain ranges (Detzel 1998; Maas et al. 2002). In these regions, the meso- and hygrophilous *T. cantans* is more common (for vicariance of the two species see e.g. Ingrisch 1981; Schiemenz 1981; Rahmel et al. 1990; Poniatowski & Fartmann 2006, 2008). The habitat use and distribution patterns of these two species are well analyzed, and competition between *T. cantans* and *T. viridissima* seemed to be inhibited mainly by their different climatic requirements which have led to different distribution patterns. However, the mechanisms of coexistence of *T. caudata* and one of the two other related *Tettigonia* species have not been analyzed in detail to date. *T. caudata* has a more

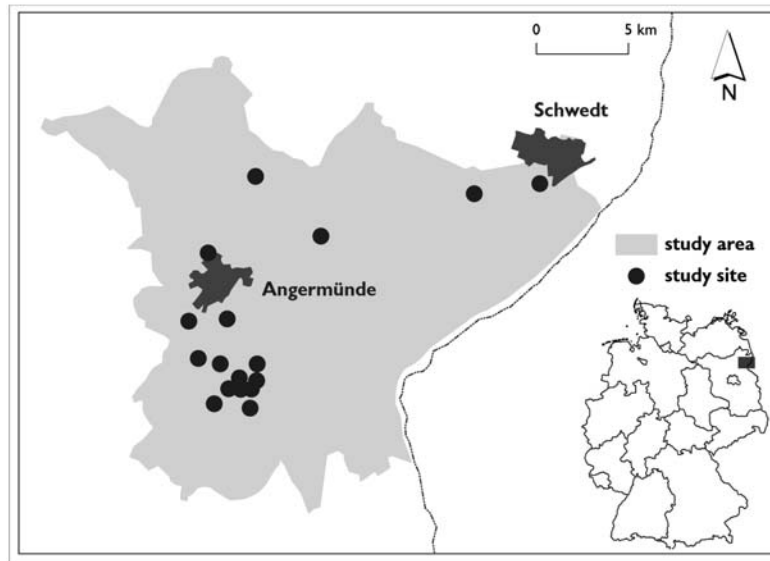


Fig. 1. Location of the study area and the 17 study sites in NE Germany.

continental distribution and reaches its range margin in NE Germany (Harz 1957; Fartmann 1997; Maas et al. 2002). In Germany, *T. caudata* always seems to occur syntopically with *T. viridissima* (Fartmann 1997; Bellebaum 2003; Schirmel & Fartmann 2007b). In this study, we analyzed how these two closely related bush-crickets can coexist. We compared the habitat use of the rare *T. caudata* and the widespread *T. viridissima* at the meso- and microhabitat level in an agricultural landscape of Northeast Germany by asking the following questions: (i) Which vegetation types (mesohabitats) and microhabitats do the species prefer? (ii) Which factors might enable coexistence?

Material and methods

The *Tettigonia* species were identified using Bellmann (2006); nomenclature followed Coray & Lehmann (1998).

Study area

The study was conducted in an agricultural landscape around the town of Angermünde (53°0' N, 14°0' E) in Brandenburg, NE Germany (Fig. 1). The climate in this region has a transitional character from Atlantic to continental with relatively dry and hot summers (mean temperature in January/August: -0.9°C/19.0°C; mean annual precipitation: 536 mm) (Müller 2002). The landscape is characterized by several glacial forms including various waterbodies, hills (up to 125 m a.s.l.), and corrugated plains on mainly loamy and sandy soils (Meynen & Schmithüsen 1961). Agriculture is the predominant land-use type (Flade et al. 2003).

Sampling

Mesohabitats

In total, 17 study sites were selected, ranging from low-growing dry grassland to very dense and highly vegetated fallows. Sites were chosen based on known occurrences of both species (Fartmann 1997; Haupt 1997; Bellebaum 2003). Per study site 1–8 plots (47 in total) were sampled. Each plot had a homogeneous vegetation structure and measured 500 m², except for linear habitats such as fringes and field margins, which were 200 m².

Vegetation was sampled twice in summer (mid-July and end of August) at three randomly chosen sub-plots (1 m²) per plot. Cover of total vegetation, herbal layer, cryptogams, and bare soil was estimated (%) as the vertical projection of each layer on the ground. The height of herbal layer, litter, and cryptogams was measured (cm). Vegetation density was estimated (%) as the vertical projection at 0–10, 10–30 and 30–50 cm field layer height (Sundermeier 1998). For statistical analyses, the values of the different heights were summed up, resulting in one vegetation density parameter (maximum = 300%).

Bush-crickets were counted between 07 and 25 July 2006. Each plot was visited once between 4:00 and 10:00 p.m. under favorable weather conditions (sunny, calm) and slowly paced off in loops, counting all singing males.

Microhabitats

Microhabitats of singing males were sampled between 02 and 28 July 2006. Between 4:00 and 10:00 p.m. on 23 observation days (sunny, calm) a systematic search for *Tettigonia* males was conducted along pathways and roads within the study area (for a map of investigated pathways see Appendix 1). When a singing male was detected, the following parameters were recorded within 1 m² around the locality of the individual: Cover (estimated in %) of total vegetation and herbs; height (measured in cm) of singing site (plant), ambient vegetation, and position height of the male.

Statistical analysis

Mesohabitats

The 47 plots were classified into six vegetation types using a hierarchical cluster analysis (Bacher 1994; Jongman et al. 1995). Ward's method with the Euclidean distance measure was used and variables were z-transformed (Bacher 1994). Cluster analysis was based on the eleven vegetation parameters, always using the maximum value of the two samples in order to describe vegetation during its development peak. Differences among vegetation types were analyzed using an ANOVA on ranks.

Effects of vegetation type on abundances of *T. viridissima* and *T. caudata* were tested using Poisson Generalized Linear Mixed-effects Models (GLMM) with *site* as a random effect (R package lme4, Bates et al. 2011). Poisson GLMMs

Table 1. Characteristics of the six classified vegetation types (cluster analysis). Data based on vegetation sampling of 47 plots within the study area in NE Germany. Shown are means and SD. Differences among vegetation types were tested using an ANOVA on ranks.

N	Vegetation type						H	P
	1 (11)	2 (14)	3 (3)	4 (5)	5 (4)	6 (10)		
Cover (%)								
Total vegetation	99.6 ± 0.8	98.9 ± 2.1	85.0 ± 5.0	86.0 ± 7.4	91.3 ± 4.8	92.3 ± 3.1	31.615	< 0.001
Herbal layer	90.0 ± 5.5	89.3 ± 6.2	81.7 ± 2.9	48.0 ± 11.0	43.8 ± 21.4	76.0 ± 13.7	25.397	< 0.001
Litter	93.8 ± 3.8	84.1 ± 13.0	38.3 ± 2.9	74.0 ± 14.7	20.0 ± 17.8	54.0 ± 26.0	29.036	< 0.001
Cryptogams	17.7 ± 26.1	10.4 ± 10.6	0	1.4 ± 2.2	68.8 ± 8.5	0.4 ± 0.8	29.969	< 0.001
Bare soil	1.1 ± 2.0	1.1 ± 2.1	18.3 ± 2.9	14.0 ± 7.4	16.3 ± 13.2	8.7 ± 5.0	28.739	< 0.001
Height (cm)								
Herbal layer	129.5 ± 22.0	118.2 ± 23.2	120.0 ± 40.0	98.0 ± 22.8	72.5 ± 15.0	29.8 ± 17.9	28.638	< 0.001
Litter	18.6 ± 4.5	7.8 ± 3.7	2.3 ± 0.6	5.8 ± 2.2	1.8 ± 1.0	3.4 ± 2.4	31.410	< 0.001
Cryptogams	1.1 ± 0.7	1.0 ± 0.6	0	0.4 ± 0.5	1.3 ± 0.5	0.1 ± 0.3	23.341	< 0.001
Vegetation density (%)								
0–10 cm	100 ± 0.0	97.1 ± 6.1	85.0 ± 8.7	84.0 ± 8.2	45.0 ± 20.8	83.0 ± 20.0	30.048	< 0.001
10–30 cm	89.1 ± 10.7	68.2 ± 25.0	76.7 ± 15.3	47.0 ± 13.0	17.5 ± 13.2	26.0 ± 21.4	30.978	< 0.001
30–50 cm	54.5 ± 15.9	34.3 ± 21.5	68.3 ± 29.3	13.0 ± 6.7	4.3 ± 1.5	3.8 ± 9.3	33.463	< 0.001
Description	Old fallows and low-intensity grasslands with very dense and high vegetation	Fallows, grasslands, and fringes, and field margins with dense and high vegetation	Young fallows (<i>Cirsium arvense</i>) with high vegetation and a high proportion of bare soil	Fringes and field margins with vegetation of intermediate height and density	Less productive, semi-dry grasslands with a high proportion of cryptogams	Intensively used (> two times mown per year) grasslands, and fringes		

were also used for testing effects of mesohabitat parameters on species abundance. Fixed effects included in the models were: cover of total vegetation, litter, cryptogams, height of herbal layer and vegetation density with *site* as a random effect. Backward selection using the Akaike information criteria (AIC) was applied in order to find the optimal model (Zuur et al. 2010). Pseudo R^2 was calculated for each model to measure the goodness of fit (Dobson 2002).

Microhabitats

Differences between microhabitat parameters of both species were tested with Gaussian GLMs. Data was $\log(x + 1)$ transformed prior to GLM analysis. The significance levels were Bonferroni-corrected to $P < 0.0125$. For both species, regression analyses were performed to analyze the relation between the height of ambient vegetation and the position of males.

All statistical analyses were performed with the software R (R Development Core Team 2011).

Results

Mesohabitats

Classification by cluster analyses revealed six vegetation types, which differed primarily in terms of height and density, decreasing from type 1 to 6 (Table 1). The vegetation types 1–3 mainly contain (very) dense and high fallows and grasslands; fringes and field margins with an intermediate height and density were grouped into type 4; type 5 consists of semi-dry grasslands with sparse vegetation and a high proportion of cryptogams; and type 6 consists of intensively used grasslands.

T. viridissima ($n = 43$) was present in 12 of the 47 plots (26%), while *T. caudata* ($n = 14$) only occurred in

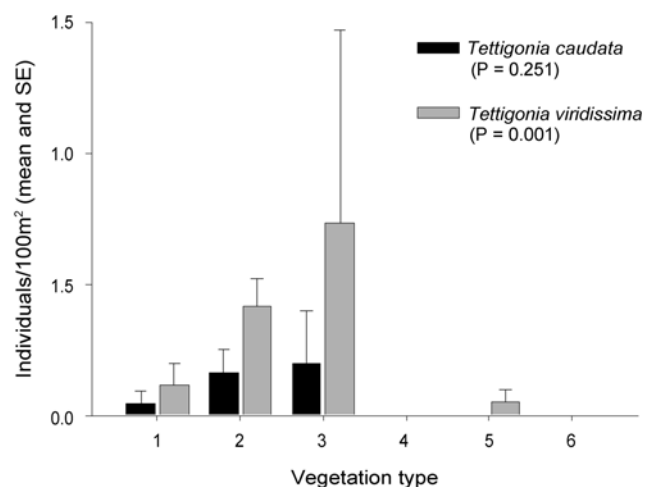


Fig. 2. Abundances (mean individuals/100 m² ± SE) of *Tettigonia caudata* and *T. viridissima* in six vegetation types, from dense (type 1) to open/low (type 6) vegetation. Differences were tested using GLMMs with *site* as a random effect.

5 plots (11%). Both species were most abundant in the dense and high vegetation types 2 and 3, but differences were significant only for *T. viridissima* (Fig. 2). The two species showed low densities in type 1 (with very high and dense vegetation), and, with the exception of a single *T. viridissima* individual in vegetation type 5, they were absent in the more open and low-growing vegetation types 4–6.

Height of field layer had a positive effect on *T. caudata* abundances, while litter cover showed a neg-

Table 2. Effects of mesohabitat parameters on abundances of *Tettigonia caudata* and *T. viridissima* based on GLMMs with *site* as a random factor. Optimal models were selected using the AIC, the goodness-of-fit of the models is shown as the residual deviance by calculating pseudo R^2 .

	<i>Tettigonia caudata</i> ($R^2 = 28\%$)				<i>Tettigonia viridissima</i> ($R^2 = 52\%$)			
Random effect	Variance		SD		Variance		SD	
Site	10.79		3.29		5.38		2.32	
Fixed effects	Estimate	SE	z	P	Estimate	SE	z	P
Litter cover	-0.04	0.03	-1.25	0.210	-0.03	0.01	-2.83	0.005
Height field layer	0.06	0.02	2.38	0.017	0.03	0.01	2.65	0.008
Vegetation density					0.02	0.01	2.78	0.006

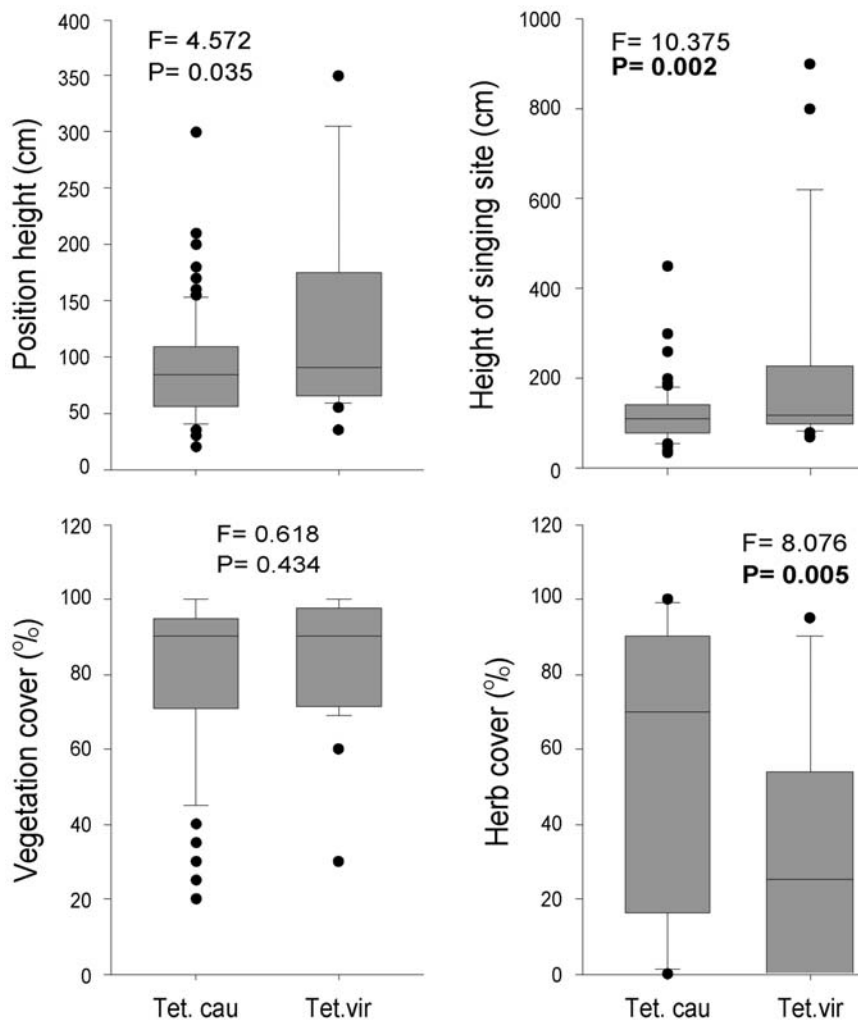


Fig. 3. Comparison of microhabitat parameters between *Tettigonia caudata* and *T. viridissima*. Differences were tested using Gaussian GLM with $\log(x + 1)$ transformed data. The significance levels were Bonferroni-corrected to $P < 0.0125$. Significant results are shown in bold.

active relationship (Table 2). Abundance of *T. viridissima* showed similar responses to mesohabitat parameters and was also positively related to vegetation density.

Microhabitats

In total, 28 microhabitats of *T. caudata* and 84 of *T. viridissima* were sampled. *T. caudata* used significantly

lower plants than *T. viridissima* as singing sites, while herb cover was significantly higher in microhabitats of *T. caudata* (70% compared to 25%; Fig. 3). No differences were observed in the position of the singing males or in vegetation cover.

Singing males of both species mainly occurred in the upper third of the vegetation (Fig. 4). For both species there was a significantly positive relationship

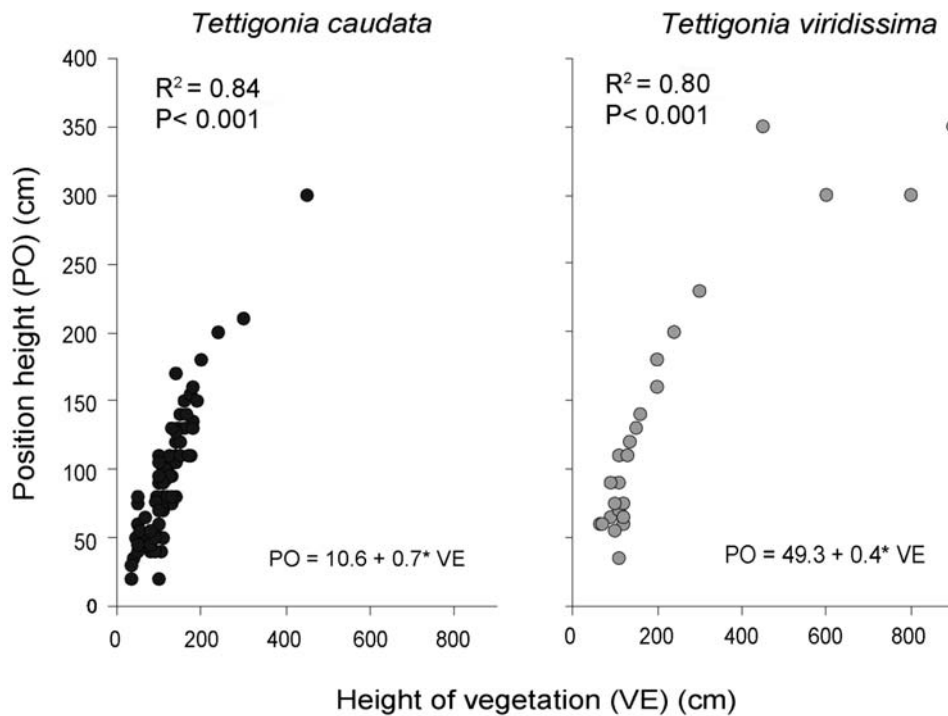


Fig. 4. Position of *Tettigonia caudata* ($n = 84$) and *T. viridissima* ($n = 28$) males in relation to ambient vegetation height. Significant results are shown in bold.

between the height of the vegetation and the position of the singing males.

Discussion

Both the competition exclusion concept (Hardin 1960) and the niche theory (Hutchinson 1957) predict that two closely related species have to differ (at least slightly) ecologically if they are to coexist in a certain habitat. In our study, the analyzed bush-cricket species *Tettigonia caudata* and *T. viridissima* differed only very marginally in their mesohabitat use (i.e., preference for vegetation types) but in several aspects of their microhabitat use.

Mesohabitats

Both species prefer similar mesohabitats and showed similar abundance patterns in the six vegetation types. Nevertheless, *Tettigonia viridissima* was more widespread in the study area and all occupied *T. caudata* habitats were also colonized by *T. viridissima*. *T. viridissima* is known to be a eurytopic species which settles in a broad range of open habitats (e.g., Sanger 1977; Detzel 1998). A syntopic occurrence of both species has already been described for Central Europe (Germany: Bellebaum 2003; Schirmel & Fartmann 2007b; Switzerland: Nadig 1991; Slovakia: Kriřtın et al. 2007).

The preferred mesohabitats of both species were characterized by dense and high vegetation (types 2 and 3). In these habitats, the large Ensifera (length: 22–44 cm; Detzel 1998) are able to find shelter, adequate food supply, and suitable singing and oviposition sites. Especially for the latter, habitats with a

very dense vegetation and a high proportion of litter, as found in vegetation type 1, seemed to be less relevant, as the species lay their eggs in the soil (c.f. Schirmel & Fartmann 2007a). Mesohabitats with shorter swards (< 100 cm) and less total-vegetation cover (< 85%) were avoided by both species (c.f. for *T. viridissima*: Oschmann 1973). These findings are supported by the GLMM analysis, which showed a negative response to litter cover for the abundance of both species, but a positive relationship with vegetation height (and density in the case of *T. viridissima*). While semi-dry grasslands might occasionally be colonized, intensively used grassland with frequent mowing is inappropriate, as mowing itself increases mortality, and vegetation is kept low, which might enhance the risk of predation (e.g., Nadig 1991; Schirmel & Fartmann 2007b). Typical habitats, in particular for *T. caudata*, are (not too old) fallows, field margins and fringes with a high proportion of herbs (e.g., *Cirsium arvense*) and little bare soil.

Microhabitats

On the microhabitat scale, both species differed only slightly in habitat use. Singing males of both species occurred primarily in the upper third of dense vegetation, which seemed to be a compromise between receiving sufficient solar radiation and shelter from predators. The occurrence of the species in upper parts of plants (especially herbs) could also be due to the presence of potential prey (e.g. flower-seeking insects; own observations). Nevertheless, two important differences in microhabitat use were observed: (i) The proportion of herbs was remarkably higher in microhabitats of *T. caudata*, which could imply that herbs are a more im-

portant food supply for this species. In contrast, *T. viridissima* did not seem to depend on a high herb cover. This might explain why the latter species is able to settle in a multiplicity of habitats (see above). (ii) *T. caudata* avoids shrubs and trees (Nadig 1991), while *T. viridissima* is arbusti- and arboricolous (Arak & Eiriksson 1992). This is reflected in the choice of higher singing sites observed in this study. The fact that position did not differ between the two species might be explained by the time of sampling (until 10 p.m.) in this study. Stridulation activity of *T. viridissima* peaks in the late evening or at night (Schirmel & Fartmann 2007b) and in cool nights, in particular, males climb up high to warmer regions of treetops or higher shrubs (Nielsen 1938). In contrast, *T. caudata* showed the highest stridulation activity in the afternoon and early evening with higher temperatures (Schirmel & Fartmann 2007b). These adaptations present a form of spatial and behavioral segregation and might further reduce possible reproduction interferences (e.g. signal jamming; see Gröning & Hochkirch 2008).

Besides the detected differences in microhabitat use, there might be differences between the two species in other life cycle stages. Since larval habitats did not seem to differ (own unpublished data) and neither did annual activity (Schirmel & Fartmann 2007b), the main variation might be found during egg development. *T. caudata* eggs are adapted to dry and hot conditions while *T. viridissima* eggs require more water for development (Ingrisch 1988). In addition, *T. caudata* are able to place their eggs deeper in the soil due to their longer ovipositor (up to 38 mm, *T. viridissima* up to 32 mm; Harz 1969).

Above all, external factors such as the presence of predators could cause a decreased abundance of both species. In such cases, the carrying capacity of settled habitat might not be reached and no competition occurs. This might enable coexistence, regardless of any overlapping habitat requirements.

Conclusion

The bush-cricket species *T. caudata* and *T. viridissima* showed a preference for very similar mesohabitats. However, *T. viridissima* was more frequent, which indicates the species' ability to settle in a broad spectrum of open habitats. Microhabitats were also similar, but differed in two aspects: *T. viridissima* preferred higher singing sites, and the herb cover was higher in microhabitats of *T. caudata*. The observed differences in microhabitats might explain the co-occurrence of the closely related bush-cricket species in open habitats. However, variation between the two species might also take place during other life-cycle stages such as egg development.

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Appendix 1. Investigated pathways and roads (black lines) with microhabitat samples of *Tettigonia caudata* and *T. viridissima* in the study area around Angermünde, NE Germany.