J Insect Conserv (2016) 20:781–788
DOI 10.1007/s10841-016-9909-3

ORIGINAL PAPER

Genista dwarf shrubs as key structures for a Mediterranean grasshopper species on alluvial gravel banks

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Received: 31 May 2016 / Accepted: 29 August 2016 / Published online: 10 September 2016

Abstract Natural floodplains belong to the most species-rich ecosystems worldwide. However, over the last decades there has been a strong decrease in the extent of natural floodplains. As a consequence, the biodiversity of these ecosystems has experienced a dramatic decline. In this study, we investigated the habitat and food preferences of the grasshopper species *Chorthippus binotatus* on gravel banks of a nearly natural river system in the Spanish Pyrenees. The studied plots on the alluvial gravel banks in the Spanish Pyrenees were characterised by strong differences in habitat structure. However, *C. binotatus* only occurred in sparsely-vegetated sub-Mediterranean dry grasslands. The abundance of the grasshopper species was also strongly related to habitat structure and cover of the main food source and dominant plant species of these open grasslands, the dwarf shrub *Genista scorpius*. Concerning habitat structure, the grasshopper species preferred habitats with sparse and low-growing vegetation with a high cover of bare ground and gravel/stones. *C. binotatus* occupies a very narrow ecological niche within the studied floodplain. It requires sparsely-vegetated gravel banks that ensure sufficient oviposition sites and a favourable ambient temperature for optimal development. *G. scorpius* dwarf shrubs have to be considered as multi-functional key elements in the habitats of *C. binotatus*. They offer high-quality food, shelter against predators and allow thermoregulation in a hot and dry Mediterranean environment. For the conservation of *C. binotatus*, we recommend maintaining and restoring both natural floodplain dynamics as well as traditional grazing systems.

Keywords *Chorthippus* · Disturbance · Dynamic habitat · Food specialisation · Land-use change · Orthoptera

Introduction

Natural floodplains belong to the most species-rich ecosystems worldwide (Ward et al. 1999; Tockner and Stanford 2002). However, over the last decades, there has been a strong decrease in the extent of natural floodplains due to human-induced changes of their disturbance regime (Tockner and Stanford 2002). As a consequence, natural floodplains are, due to their role as biodiversity hotspots and threat status, protected under the Habitats Directive of the European Union (EC 2007). In Europe, for example, about 90 % of the alpine rivers are strongly modified due to human flood control and hydropower production (Tockner et al. 2008). Naturally, alpine rivers are characterised by a high level of hydrogeomorphical dynamics and spatio-temporal habitat heterogeneity, but also microclimatic heterogeneity (Ward et al. 1999; Arscott et al. 2001; Tockner et al. 2008). These diverse conditions facilitate the occurrence of many highly specialised insect species (e.g. Reich 1991; Kuhn 2005; Lemke et al. 2010; Maag et al. 2013; Münsch et al. 2013). A key aspect of riverine ecology is the question of how species survive in those disturbance-dominated

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ecosystems, as they are regularly subjected to a severe loss of resources and substantial habitat change due to disturbance (Reich 1991).

Orthoptera respond rapidly to environmental changes and, thus, are often used as indicator organisms (Bazelet and Samways 2012; Fartmann et al. 2012; Helbing et al. 2014; Adu-Acheampong et al. 2016). In Europe, land-use changes caused a strong decline of Orthoptera species diversity due to the loss or degradation of their habitats (Marini et al. 2009; Poniatowski and Fartmann 2010; Maag et al. 2013). Therefore, Orthoptera have recently received growing attention in conservation biology (e.g. Wünsch et al. 2012; Helbing et al. 2014). The most important determinants for the occurrence of Orthoptera are vegetation structure (Gardiner et al. 2002; Poniatowski and Fartmann 2008) and microclimate (Willott and Hassall 1998; Gardiner and Dover 2008). In contrast to other insect groups (e.g. Auchenorrhyncha: Nickel 2003; Lepidoptera: Munguira et al. 2009), food-availability seems to play a minor role in the habitat selection of Orthoptera as most species are polyphagous (Ingrisch and Köhler 1998). However, food availability and predation are also often interrelated with the aforementioned factors, and may become important for Orthoptera in sparsely-vegetated habitats (Belovsky and Slade 1993; Wünsch et al. 2012; Helbing et al. 2014). Under natural conditions, alluvial gravel banks are characterised by a spatial mosaic of different successional stages which allow the coexistence of many specialised Orthoptera species (Helbing et al. 2014). The importance of alluvial gravel banks as a habitat for Orthoptera has recently been shown in some studies (e.g. Reich 1991; Maag et al. 2013; Münsch et al. 2013; Helbing et al. 2014). However, until now, there is often a lack of detailed knowledge on the habitat requirements of Orthoptera species of conservation concern in these ecosystems.

In this study, we investigated the habitat and food preferences of the grasshopper species *Chorthippus binotatus* on gravel banks of a nearly natural river system in the Spanish Pyrenees. The species has a small west-Mediterranean range where it is partly endangered (Sardet and Defaut 2004). Except for a few anecdotal data (e.g. Poniatowski et al. 2009; Krämer et al. 2010), there is no information available on the ecology of this species from the core of its range, the Iberian Peninsula. In particular, we raised the following questions:

1. Which are the key structures that determine the abundance of *C. binotatus* on alluvial gravel banks?
2. Which ecological functions can be assigned to these key structures?
3. How would the species respond to alterations of floodplain dynamics?

Materials and methods

Study species

Chorthippus binotatus (Fig. 1a) is a xero-thermophilous grasshopper species with a small west-Mediterranean range extending from Morocco, the Iberian Peninsula to western and southern France (Sardet et al. 2015; Eades et al. 2016). In the Pyrenees, the species is widespread, but generally not very abundant (Poniatowski et al. 2009); here, it prefers stony and shrub-rich dry grasslands (Krämer et al. 2010). The species' diet clearly differs from those of other grasshopper species of the genus *Chorthippus. C. binotatus* feeds oligophagously on shrubby legumes, whereas all other *Chorthippus* species are known to be gramnivorous (Picaud et al. 2002, 2003).

Study area

The study area is located in the western Spanish Pyrenees about 10 km west of Jaca (province Huesca) in the Aísa Valley which is shaped by the braided alpine river Río Estarrún.

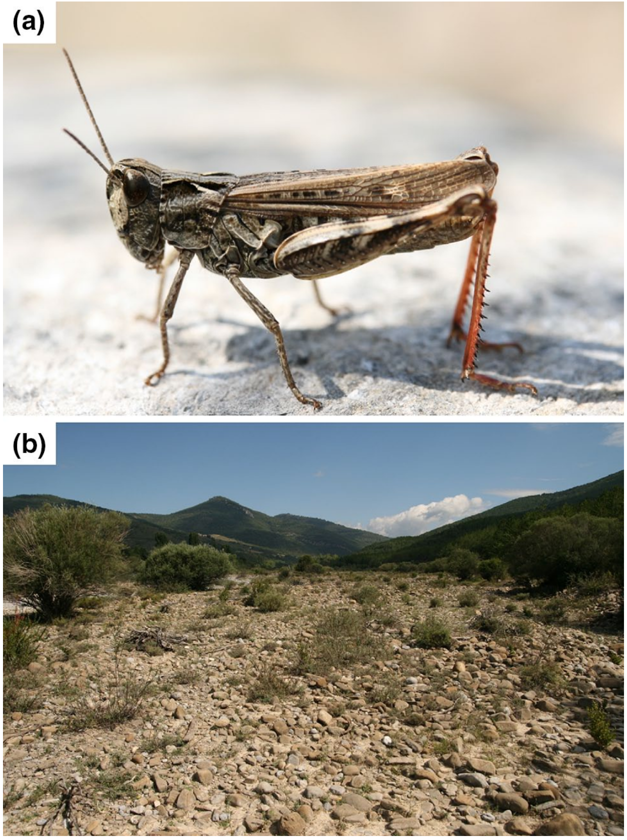

Fig. 1 **a** *Chorthippus binotatus* thermoregulation: to avoid overheating, the grasshopper stretches its legs to reach the maximum distance between the hot stone and its body. **b** Sparsely-vegetated gravel banks with *Genista* dwarf shrubs are the characteristic habitats of *C. binotatus*

It covers a 12 km long part of the lower valley of the river at an elevation of 700–1050 m a.s.l. The supra-Mediterranean climate in the study area is characterised by a mean annual temperature of 9.8 °C and an average annual precipitation of 835 mm (Aísa 1050 m a.s.l.). The summer months between June and September are very warm and dry; hot periods reaching temperatures of up to 40 °C can occur. During summer time, the poorly vegetated gravel banks in the floodplain tend to heat up significantly and the river temporarily dries up under extreme weather conditions (pers. observation). In winter and spring, the precipitation strongly increases with up to 100 mm of rainfall per month. Within the study area, the Río Estarrún is interrupted by a weir; further regulatory measures, however, are missing. Despite the weir, the river system is highly dynamic and regularly influenced by flooding events. Hence, the floodplain can be described as a nearly natural ecosystem consisting of mosaics of different successional stages (Münsch et al. 2013). The most characteristic vegetation types on the gravel banks are pioneer vegetation, sub-Mediterranean dry grasslands (*Aphyllanthion*), with *Genista scorpius* being the dominant plant species (Fig. 1b), as well as willow shrubs (*Salicion albae*) and barberry shrubs (*Berberidion vulgaris*) (Villar et al. 1997).

Study plots

In August 2010, we studied 57 randomly selected plots. The plots covered the complete range of potential habitats of *C. binotatus* on the gravel banks of the study area from pioneer vegetation, over dry grasslands and shrubby grasslands to open shrubland. Plots were characterised by a homogeneous vegetation structure (Poniatowski and Fartmann 2008) and a size of at least 500 m² to avoid edge effects (Schirmel et al. 2010).

Sampling of *Chorthippus binotatus*

The sampling of *C. binotatus* was conducted once in the second half of August 2010 using transect counts. This method belongs to the most commonly used sampling techniques for Orthoptera (Gardiner et al. 2005) and, in contrast to sweep-netting or the use of a box quadrat, it can be applied even in vegetation rich in dwarf shrubs (Gardiner and Hill 2006). All plots were systematically scanned for individuals of *C. binotatus* by walking in loops with a total length of 100 m at each plot. All visually and acoustically detected individuals at a distance of up to 0.5 m on both sides of the transect were counted (total observed area per plot: 100 m²). Individuals which could not directly be identified were caught by sweep net or hand and released after determination in the field. The loops had a distance of 5 m from each other to avoid double counting of individuals. Surveys were conducted under favourable weather conditions (warm, sunny and calm days) between 10:00 and 17:00 h. Species were identified according to Poniatowski et al. (2009).

Table 1 Overview of sampled environmental parameters and their statistical analysis

Sampled parameter	Factor level	Statistics	Mean (±SE)	Min.–max.
Response variables				
Density (individuals/100 m²)	Metric	GLM	2.2 ± 0.3	0.0–12.0
Predictor variables				
Cover (%)				
Total vegetation*	Metric	GLM, PCA	50.3 ± 3.0	15.0–100.0
Shrub layer	Metric	GLM, PCA	9.3 ± 1.3	0.0–40.0
Genista dwarf shrubs	Metric	GLM	18.7 ± 1.3	2.5–45.0
Herb layer*	Metric	GLM, PCA	22.7 ± 3.1	2.5–85.0
Grasses*	Metric	GLM, PCA	14.5 ± 2.6	0.0–80.0
Herbs*	Metric	GLM, PCA	7.2 ± 0.8	2.5–30.0
Mosses/lichens	Metric	GLM	1.3 ± 0.3	0.0–10.0
Gravel/stones**	Metric	GLM, PCA	34.0 ± 3.1	0.0–75.0
Bare soil**	Metric	GLM	9.3 ± 1.6	0.0–70.0
Vegetation density (%)*	Metric	GLM, PCA	20.5 ± 2.4	1.7–69.2
Vegetation height (cm)*	Metric	GLM, PCA	30.2 ± 1.3	0.0–55. 0

GLM generalised linear model, *PCA* principal component analysis, *SE* standard error, *Min.* minimum, *Max.* maximum

*Due to strong inter-correlations ($r_s > 0.5$, $p < 0.05$) vegetation height, vegetation density, as well as the cover of total vegetation herbs, grasses were merged to a new variable called 'vegetation structure' using a PCA

**Due to strong inter-correlations ($r_s > 0.5$, $p < 0.05$) the cover of gravel/stones and bare soil were merged to a new variable called 'bare-ground structure' using a PCA

Environmental parameters

After the sampling of *C. binotatus*, we ascertained environmental parameters in a randomly selected undisturbed part of the plot with a size of 3 × 3 m (Table 1). We recorded the following parameters of the horizontal vegetation structure (in 5 % steps): cover of total vegetation, shrub layer, herb layer, dwarf shrubs, herbs, grasses, mosses, litter, gravel, stones and bare soil. In cases where cover was above 95 % or below 5, 2.5 % steps were used. The average vegetation height in the plots was measured at an accuracy of 2.5 cm. Vegetation density was estimated using a 50 cm wide and 30 cm deep wire-framed box, which was open on all sides except the back. Horizontal wires on the front side of the box divided it into six layers (0–5, 5–10, etc. up to 25–30 cm). The cover of each layer was viewed horizontally against the bright back of the box, using the same classes as for the horizontal structure (Poniatowski and Fartmann 2008; Fartmann et al. 2012).

Food-preference experiments

During the study period, we conducted a laboratory experiment analysing the food preferences of *C. binotatus*. In total, we studied the feeding preferences of 48 experimental units. To this purpose, we captured 48 adults with a balanced sex ratio (24 ♂♂ vs. 24 ♀♀) in the study area. According to Picaud et al. (2003), all individuals were individually kept under identical conditions for 4–6 h without food supply in transparent plastic boxes covered with dark nylon gauze (500 cm³) before the experiments were started. We chose four experimental food plants which belong to the most abundant plant species in the study area: *Dorycnium pentaphyllum, G. scorpius, Molinia caerulea* and *Thymus vulgaris*. In each experimental unit, leaf material of the food plants was given simultaneously and in equal quantity (covering a size of 0.5 cm²) to the ground of the boxes. The food material was arranged in rows. The order of the food plants in the rows was randomised between the experimental units to minimise the effect of confounding variables. According to Picaud et al. (2003), we counted feeding frequencies with respect to the food plants for each individual over a time period of 15 min. The feeding frequencies were observed by counting food intakes of the individuals. If an individual stopped feeding on a plant sample and changed to another food plant, we counted it as a discrete unit of food intake.

Statistical analysis

To assess which environmental parameters explain the abundance of *C. binotatus*, multivariate generalised linear models (GLM) were conducted (Crawley 2007) (Table 2). Non-significant predictors were excluded by stepwise backward selection by AIC values from the final model. To deal with multicollinearity, we summarised parameters prior to GLM analysis using PCA (Table 1, cf. Helbing et al. 2014). Significances and regression curves fitted on the scatterplots were calculated using univariate GLM. All significances in the models were ascertained using Wald tests.

Table 2 Relationship between the densities of *Chorthippus binotatus* (individuals/100 m²) and the predictor variables (Table 1)

Parameter	Estimate	SE	Z	P
(Intercept)	–0.43	0.36	–1.20	n.s
Vegetation structure	–0.81	0.23	–3.48	***
Cover *Genista scorpius* (%)	0.05	0.01	5.23	***
Bare-ground structure	0.28	0.11	2.50	*
Shrubs	–0.04	0.02	–2.18	*

The significances and model accuracy were tested using multivariate generalised linear models (GLM) with a Poisson error structure (N = 57). Non-significant environmental parameters were excluded by backward-stepwise selection

Nagelkerke's Pseudo $R^2 = 0.87$. Significance levels are indicated as follows: *n.s.* not significant; *$p < 0.05$; ***$p < 0.001$

We compared feeding frequencies between the four food plants using repeated measures ANOVA. Pair-wise comparisons following ANOVA were performed using paired t-test. Statistical analyses were performed using R-3.2.2 (R Development Core Team 2016), SPSS 23.0 and SigmaPlot 12.5 statistical packages.

Results

Habitat preferences

Chorthippus binotatus was widespread in the study area, but typically occurred in low abundance (Table 1). Altogether 37 of the 57 studied plots were occupied by *C. binotatus*. On these sites, we detected 119 individuals of the species; the maximum density was 12 individuals per 100 m² (Table 1). All occupied plots were sub-Mediterranean dry grasslands belonging to the *Aphyllanthion*. The density of *C. binotatus* was significantly affected by vegetation and bare-ground structure (Fig. 2; Table 2). We found the highest abundance in sparsely-vegetated and low-growing habitats with a high cover of bare ground and gravel/stones. Furthermore, the density of *C. binotatus* was positively correlated with the cover of *G. scorpius* dwarf shrubs. A higher abundance (3 or more individuals/100 m²) of the grasshopper was only observed when the cover of the legume was at least 10 % (Fig. 2b). Plots with a cover of 35 % of the dwarf shrub or more were always occupied by *C. binotatus*. In addition, grasshopper abundance decreased with the cover of shrubs. Plots with a shrub cover of more than 30 % were never occupied by *C. binotatus* and high densities

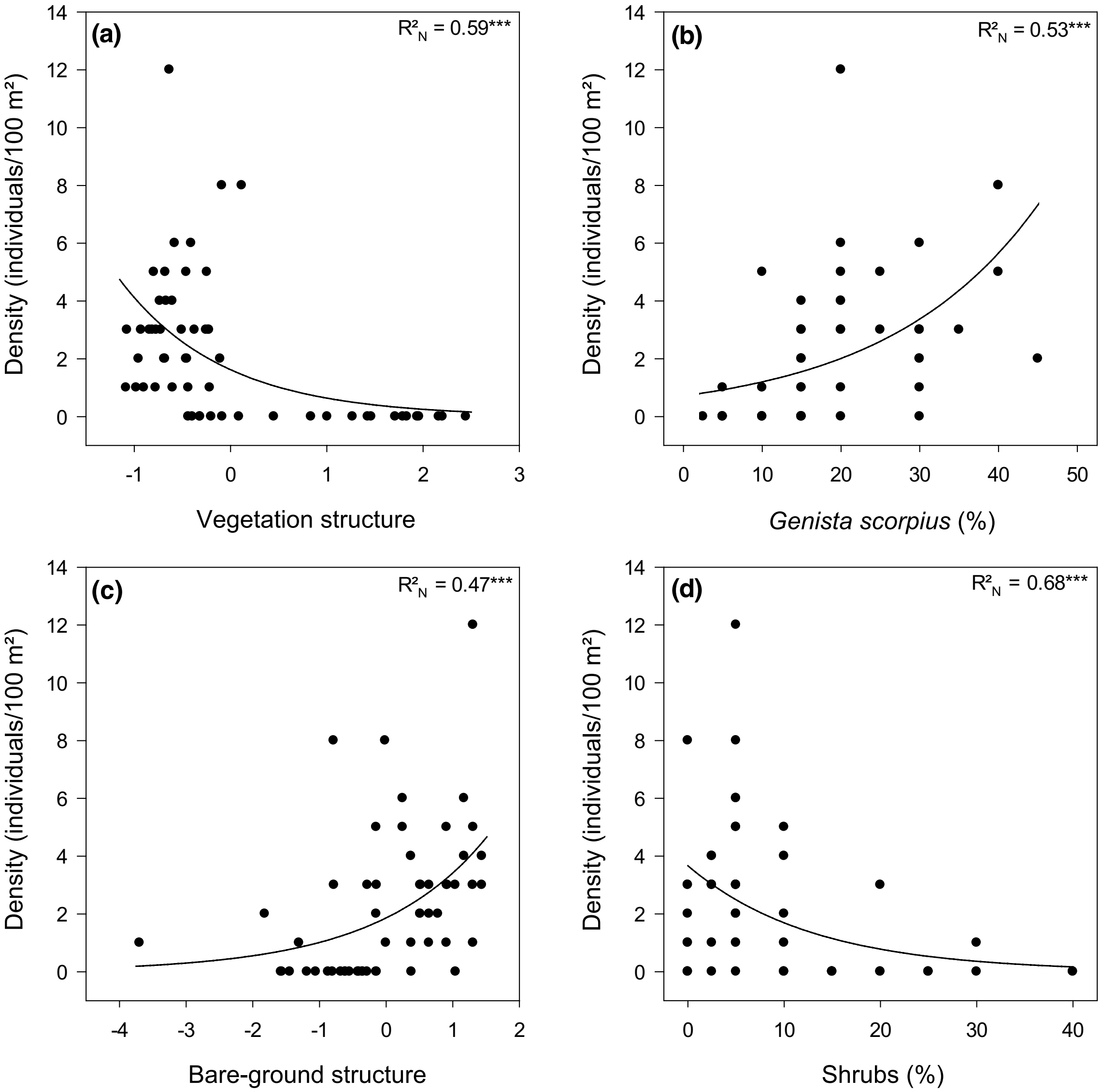

Fig. 2 Relationship between the densities of *Chorthippus binotatus* (individuals/100 m²) and significant environmental parameters assessed in the multivariate GLM (Table 2): **a** vegetation structure; **b** *Genista* dwarf shrubs (%); **c** Bare-ground structure; **d** shrubs (%). The significances and model accuracy presented in the figures were tested using univariate generalised linear models (GLM) with a Poisson error structure (N = 57). Significance levels are indicated as follows: *n.s.* not significant; ***$p < 0.001$

(>3 individuals/100 m²) were only found if shrub cover reached at least 10 %. The variance explained in the data set by these variables was high, in both the univariate models (Nagelkerke Pseudo-R^2 >0.47) and the multivariate one (Nagelkerke Pseudo-R^2 = 0.87).

Food preferences

In our food-choice experiments, we observed 102 food intakes belonging to 48 individuals of *C. binotatus*. By far the highest feeding frequencies were detected for *G. scorpius* with 55 % of all food intakes significantly differing from those of the three other food plants (Fig. 3). The feeding rates on the other plant species were low (*D. pentaphyllum* 16 %, *T. vulgaris* 13 %, and *M. caerulea* 17 %).

Discussion

The studied plots on the alluvial gravel banks in the Spanish Pyrenees were characterised by strong differences in habitat structure ranging from pioneer vegetation, over dry grasslands and shrubby grasslands to open shrubland. However, *C. binotatus* only occurred in sparsely-vegetated sub-Mediterranean dry grasslands of the *Aphyllanthion*.

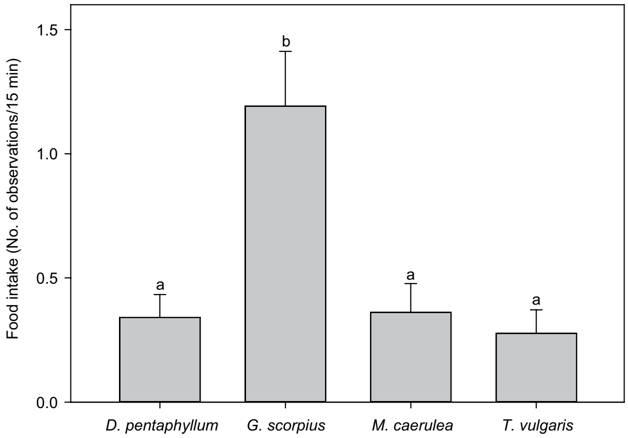

Fig. 3 Feeding frequencies observed in laboratory experiments (N = 48). Comparison of four plants: *Genista scorpius, Dorycnium pentaphyllum, Thymus vulgaris* and *Molinia caerulea*. Differences between the four species were tested using repeated measures ANOVA. *Different letters* indicate significant differences of pairwise comparisons (paired *t* test, $p < 0.05$)

The abundance of the grasshopper species was also strongly related to habitat structure and the cover of the main food source and dominant plant species of these open grasslands, the dwarf shrub *G. scorpius*. Concerning habitat structure, the grasshopper species preferred habitats with sparse and low-growing vegetation with a high cover of bare ground and gravel/stones.

Open gravel banks are characterised by a dry and hot microclimate (Stoutjesdijk and Barkman 1992; Lemke et al. 2010), which are conditions that are generally known to favour the growth and development of thermophilous Orthoptera species (Chappell and Whitman 1990; Willot and Hassall 1998; Gardiner and Dover 2008). Moreover, such gravel banks offer a sufficient amount of sunlit bare soil as potential oviposition sites for *C. binotatus*. Lemke et al. (2010) showed for the related species *Chorthippus pullus*, in floodplains of the Bavarian Alps, that sun-exposed soil is a crucial habitat component. However, due to the very sparse vegetation on open gravel banks, the food supply for Orthoptera is limited and there is also a lack of hiding sites in which to escape predators (Helbing et al. 2014). Both factors can be assumed to constrain the occurrence of *C. binotatus* on the open gravel banks of the study area, too. Besides this, the gravel and open soil can heat up very strongly during warm and sunny summer days (Stoutjesdijk and Barkman 1992), so that the sites might even become too hot for the grasshopper species. Overheating can be a problem for Orthoptera in open habitats during summer; this has even been shown under the less extreme macroclimatic conditions of North-western and Central Europe (Willott 1997; Wünsch et al. 2012). However, habitats that are too shady with a cooler microclimate were also avoided, which is what one would expect in a Mediterranean insect species. Plots with a shrub cover of more than 30 % were never occupied by *C. binotatus*.

In our study, *G. scorpius* dwarf shrubs played a crucial role for *C. binotatus*. The food-choice experiments showed that the legume was clearly the preferred food plant of the species. Such a close dietary relationship to a specific plant species is a rather uncommon phenomenon in Orthoptera. According to Joern (1979) specialisation on a single food plant usually occurs only when the food plant is abundant and their occurrence is predictable in space and time. *G. scorpius* was the dominant plant species in the habitats of *C. binotatus* and a predictable food source as it is long-lived and evergreen (Villar et al. 1997). During hot summer periods, the groundwater level is very low and the gravel banks heat up strongly (cf. "Study area" section). As a result, plant growth and photosynthesis are very limited in most plant species. In contrast, *G. scorpius* has a high drought tolerance and is still vital due to its deep root system, even on permeable and dry gravel banks (Valladares et al. 2003; Hernandez et al. 2010).

Orthoptera are not only affected by the availability of sufficient food, but also by their quality (Joern and Behmer 1998; Ritchie 2000). According to Picaud et al. (2003) *C. binotatus* responds positively to food resources which are rich in nitrogen. Legumes are able to fix nitrogen due to the mutualistic relationship with *Rhizobium* bacteria; consequently, their nitrogen content is usually high (Taiz et al. 2015).

Besides the role of *G. scorpius* as the most important food source, it is a structural component of vital importance for *C. binotatus*. During the sampling of *C. binotatus*, most individuals were observed sitting on *Genista* plants some decimetres above the ground (own observation). The dwarf shrubs, with its thorny branches, probably provide effective protection against predators (e.g. birds and ground-dwelling reptiles) (cf. Belovsky and Slade 1993). Moreover, *C. binotatus* is able to regulate its body temperature to ambient temperature by adjusting its position, height, and orientation on the plant. This hypothesis is supported by the findings of O'Neill and Rolston (2007), which showed that Orthoptera tend to move from the ground to higher vegetation during hot periods. In particular, under the hot Mediterranean climate, structures that allow shade-seeking behaviour are of high importance for thermoregulation (see above).

In conclusion, *C. binotatus* occupies a very narrow ecological niche within the studied floodplain. It requires sparsely-vegetated gravel banks that ensure sufficient oviposition sites and a favourable ambient temperature for optimal development. *G. scorpius* dwarf shrubs have to be considered multi-functional key elements in the habitats of *C. binotatus*. They offer high-quality food, shelter against predators and allow thermoregulation in a hot and dry Mediterranean environment.

Implications for conservation

Under natural conditions, succession in floodplains is inhibited by periodic floods and therefore early successional stages with sparse vegetation are promoted (Ward et al. 1999). In addition, the low water level in the floodplains during the dry summer months in the Spanish Pyrenees slows down succession. In contrast, a loss of river dynamics would very likely result in an expansion of highly competitive shrubs (e.g. willow shrubs, barberry shrubs) at the expanse of open gravel banks. Hence, conditions that provide a poor habitat quality for Orthoptera in general (Helbing et al. 2014) and for *C. binotatus* in particular.

Outside the floodplains, open sub-Mediterranean dry grasslands and *C. binotatus* also occur (Villar et al. 1997; Krämer et al. 2010). However, land-use change, especially the loss of transhumance, caused a rapid decline of sub-Mediterranean dry grasslands in the Pyrenees (Garcia-Ruiz and Lasanta-Martinez 1990; Gartzia et al. 2016). We therefore recommend maintaining and restoring both natural floodplain dynamics as well as traditional grazing systems. In the light of conservation measures, it is crucial to detect specific key structures to avoid negative effects of environmental change on species of conservation concern.

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