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ORIGINAL PAPER

Mobility and microhabitat utilization in a flightless wetland grasshopper, *Chorthippus montanus* (Charpentier, 1825)

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Abstract Wetlands are among the most threatened habitat types on our planet. Their decline will probably even intensify under climate change. Many biota are strongly dependent on wetlands, including a large number of invertebrate species. The populations of such hygrophilous species become increasingly disconnected due to the ongoing fragmentation of their habitats. This is particularly true for species with reduced dispersal capacities, such as flightless insects. We studied mobility, population size and microhabitat utilization in a population of an endangered grasshopper species, the Water-meadow Grasshopper, *Chorthippus montanus*. Our mark-recapture study revealed that the cumulative movement distance of the adults was on average 23.5 m with a maximum of 104 m. The microhabitat analysis showed that both sexes of *C. montanus* preferred warmer patches with greater radiation than measured at control sites. Niche overlap among sexes was stronger than expected by chance, while niche overlap between insects and controls showed the opposite pattern. Our results suggest that *C. montanus* is strongly restricted to its habitat and is probably not able to cross larger distances through unsuitable vegetation. Hence, we assume that the populations of this flightless insect species are strongly isolated. However, the effect of the rare macropterous morph of *C. montanus* on gene flow remains unknown. Wetland restoration is crucial to reconnect the existing wetland patches in Central Europe and thereby reduce the negative effects of habitat fragmentation on wetland species.

Keywords Dispersal · Habitat preferences · Mark-recapture · Microhabitat use · Orthoptera · Wetland conservation

Introduction

Due to the strong human influence on wetland systems, these habitat types belong to the most threatened ecosystems on our planet. On a global scale, almost 50% of the wetlands have been lost and large parts are still unprotected and declining (van der Valk 2006). It is likely that their deterioration will even intensify under climate change as massive changes in their hydrology are expected (IPCC 2007). As many wetlands are centres of biodiversity and inhabited by specialized biota they are of great value for nature conservation (van der Valk 2006). Hence, it is crucial to protect wetland areas throughout the biomes in order to prevent future extinctions (Braschler et al. 2009). The main factors driving the decline and deterioration of wetland habitats are agricultural utilization or intensification of agricultural practices, draining, dams, eutrophication, pollution by toxic chemicals, invasive species and regulation of streams and rivers (Brinson and Malvárez 2002). Due to the ongoing loss of wetlands, such habitats have become increasingly fragmented (Gibbs 2000). This process reduces gene flow among populations of wetland species and decreases the chance for successful re-colonization, leading to regional extinctions (Exeler et al. 2008). As many biota are strongly dependent on wetlands, including a large number of invertebrate species, these taxa

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are particularly threatened by the loss and fragmentation of wetland habitats (Batzer and Wissinger 1996). The ongoing fragmentation is particularly problematic for species with reduced dispersal capacities, such as flightless insects (Hochkirch et al. 2007a).

Many insect species are highly specialized on their microhabitats, such as food plants (e.g. Lepidoptera, Hemiptera) or vegetation structure (e.g. Carabidae, Orthoptera). Thus, minor changes in habitat quality can lead to rapid population declines in insect species (New 2009). Sufficient knowledge on the habitat requirements and mobility of endangered insect species is, therefore, needed in order to obtain information on potential threats and develop conservation strategies. Insects are still underrepresented on the global red list of endangered species (Butchard et al. 2010). However, in some regions (particularly in industrialized countries), information on threatened insects is available and regional red lists have been published (Binot et al. 1998). As the human pressure on wetlands is particularly high in industrialized regions (Gibbs 2000), there is a strong need for conservation of hygrophilous insects in these areas. In Central Europe, wet meadows have been agriculturally used for centuries, as they belong to highly productive ecosystems (Küster 1995). During the last decades, many wet meadows have been either abandoned or drained as other agricultural techniques have become more profitable. Orthoptera are typical grassland insects and known to be good indicators for the quality of open-land habitats as they respond strongly to different management practices (e.g. Hochkirch and Adorf 2007; Jonas and Joern 2007). Approximately 50% of all Orthoptera species in Germany are considered endangered (Ingrisch and Köhler 1998a).

The Water-meadow Grasshopper, *Chorthippus montanus* (Charpentier, 1825), is endangered in many European countries (Bellmann 2006). This species is strongly dependent on constantly damp grasslands due to a low tolerance of the eggs towards desiccation (Ingrisch 1983a). Both sexes of *C. montanus* are flightless suggesting a low dispersal ability (Reinhardt et al. 2005). However, a macropterous morph of this species occurs occasionally (Kleukers et al. 1997). These factors indicate that the species may be strongly threatened by both habitat deterioration and habitat fragmentation. In order to improve the conservation management for this species, specific information on its population ecology and microhabitat preferences are needed. Here, we present a study on the mobility, population size and microhabitat utilization in a population of *C. montanus* in order to assess potential threats and develop management recommendations. We hypothesized that mobility in this flightless species is low and that the insects are strongly confined to their specific habitat. We also wanted to test the hypothesis that individuals of *C. montanus* prefer a medium vegetation height and density (Langmaack and Schrader 1997).

Methods

Study species and study site

Chorthippus montanus (Charpentier, 1825), the Water-meadow Grasshopper, is a univoltine graminivorous grasshopper species, reproducing from July to September and hibernating in the egg stage (Kleukers et al. 1997). The species occurs from Kamchatka in the east to the Atlantic Ocean in the west. In Europe, it occurs north of the Alps, the Pyrenees and Macedonia, but it is missing on the British isles, in Denmark and parts of Fennoscandia (Kleukers et al. 1997). The populations of this species are usually small and isolated as the species is restricted to wet habitats, such as water meadows, marshes, peat bogs and wet heathland. Its hygrophilous behaviour is mainly caused by the lack of tolerance for aridity of its eggs (Ingrisch 1983a). *C. montanus* is threatened by the ongoing decline and degradation of wetlands (Bellmann 2006). It is red-listed in Germany (Ingrisch and Köhler 1998a), the Netherlands (Kleukers et al. 1997), Belgium (Decleer et al. 2000), Switzerland (Thorens and Nadig 1997) and France (Sardet and Defaut 2004).

The study site, a species-rich water meadow, was chosen mid July 2009, after checking several populations in the surroundings of Trier (Rhineland-Palatinate, Germany). It is situated in a valley near Prosterath (Beuren i. Hochwald) in the Hunsrück mountains (ca. 20 km east of Trier, 49°44′6.59″N, 6°54′12.87″E; ca. 400 m a.s.l.). The water meadow is mainly surrounded by forest and has an area of 11,020 m^2, including dryer areas, in which *C. montanus* did not occur. *C. montanus* occupied an area of 4,451 m^2. The site was chosen, because (1) it seemed to maintain a large population of *C. montanus*, (2) it was extensively managed using cattle grazing, (3) the owning farmer was willing to cooperate during the whole study period. The cattle was removed during the study period.

Data collection

We applied two different methods to study the ecology of *C. montanus*. A marc-recapture study was performed in order to obtain data on population size and mobility. During each visit, individuals of *C. montanus* were caught with a net on the complete study site. Each individual was marked with a permanent non-toxic paint marker (Edding 780) using the 1-2-4-7 method (Buchweitz and Walter, 1992). The geographic coordinates for each catch were determined with a GPS device (Garmin eTrex Vista HCx) at the site, where the individual was captured (min. accuracy 3 m). Afterwards, the individual was released at the same position. Following parameters were recorded: date, number of the individual, sex and the storage location of the coordinate in the GPS. The mark-recapture study was performed on 29 days from 24 July 2009 to 28 September 2009 (i.e. every 2–3 days).

We used a microhabitat analysis in order to obtain information on microhabitat use according to the method described in Gröning et al. (2007a). Data collection took place from 17 July 2009 to 9 September 2009 at the exact location of undisturbed haphazardly chosen individuals during their activity period (09:00–17:30). Only those individuals were recorded, which showed no sign of disturbance. The sexes were chosen alternately in order to correct for time effects. During each day a new route was chosen in order to avoid pseudoreplication. Usually the next individual was already detected while the measurements of the former one were not yet finished. Following parameters were recorded: date, time, sex, behaviour, weather. Temperature was recorded using a digital infrared thermometer (Peak Tech Infrared Thermometer 4990). Radiation was measured with a luxmeter (Peak Tech Digital Lux Meter 5025), aligned horizontally above the insect. The substrate, on which the insect perched, was noted and the height of its location (perch height) was measured with a folding rule. In a circle of 30 cm diameter surrounding the insect, we measured the highest plant and estimated vegetation cover for the following components: grasses, rushes, forbs, litter and bare ground. We used a green wire hoop (diameter: 30 cm) with two transverse interconnections to achieve an estimation accuracy of 10%. As the different vegetation components may overlap, the totals may exceed 100%. We also noted the name of the two researchers recording the microhabitat data in order to test for potential bias in the data. However, no observer effect was detected (no significant interaction between observer and response variable in ANOVAs). For each individual we recorded a corresponding control sample in a distance of 1 m from the location of the insect directly after the measurements of the insects' location (the direction was chosen randomly by drawing lots). A distance of 1 m was chosen as these locations should be easily attainable for the insects (but not actively chosen). Temperature and radiation were measured at the same height as at the insect locations.

Mark-recapture analysis

Estimation of population size was operated in MARK 4.3 (White and Burnham 1999) using the module POPAN, which performs Jolly-Seber calculations and is suitable for open populations with differing death and recruitment rates over time. POPAN 5.0 estimates three parameters based upon mark-recapture data: ϕ_i is the daily residence rate as the number of individuals at the site combining mortality and emigration, p_i is the daily catchability and $pent_i$ the daily recruitment combining the percentage of birth and immigration. Based on these first three parameters B_i, the daily recruitment, N_i the total daily population size and N the total population are derived (Fric et al. 2009). We first calculated the full model (ϕ_i(g*t)p(g*t)pent(g*t)N(g); g = sex, t = time) and performed a goodness of fit test to check the quality of our data. We then calculated the predefined models and simplified them in order to reduce the number of utilized parameters. For each response variable we first used the interaction between sex and time (g*t) as explanatory variable. Then we used the addition of sex and time (g + t) and afterwards we tested sex (g) and time (t) independently. We calculated each possible combination of these factors and used the Akaike information criterion (AIC) to find the best fitting model.

Calculation of distances was operated with ArcView GIS 3.2 (ESRI) using the extensions "Animal Movement" and "Home Range Analysis". For the calculation of distances we included only individuals that were recaptured at least once (n = 320). First, the simple distance between two consecutive captures of each individual was measured. Based on these data, we calculated the daily movement for each individual. The addition of all single distances revealed the cumulative movement distance of each individual. The maximum distance between any two observations of an individual was also recorded. To test if the maximum distances differ from random distances we used the command "Generate Random Points" in the extension "Animal Movement" for our study site. Based on these random points, we calculated an equal number of random distances and compared them to the measured maximum distances in an ANOVA. The data were Box-Cox-transformed using Venables and Ripley's MASS library for R (Venables and Ripley 2002) to fit the data to the models assumptions. In order to fit a model to the cumulative movement distances, we used a curve fitting approach in Lab Fit 7.2.47 (Silva and Silva 2009).

Microhabitat analysis

Since microhabitat utilization might differ substantially among sexes (Hochkirch et al. 2007b, 2008), we performed oneway ANOVAs for metric parameters with sex as the explanatory variable (fixed effect) and date and time as covariates. As no significant interactions of sex with either date or time occurred, we did not include the main effects of date or time in the results. χ^2 cross table tests were performed for nominal data (substrate). If data distribution was not suitable for ANOVAs, the data were

Box-Cox-transformed. To test for differences in the variances associated with the means (as a measure of niche breadth, Gröning et al. 2007b), Fisher's *F* test was used (Crawley 2005). We used paired *t* tests to compare microhabitat parameters measured at the insects′ locations and the corresponding control. To find correlations among environmental parameters (i.e. vegetation structure, microclimate) and with the insects′ locations, a standardized principal component analysis (PCA) was carried out. Due to the strong variability of the scales of our data (e.g. Lux, °C), we used the function "rda" of the community ecology package vegan 1.17–4 for R (Oksanen et al. 2010) to scale the factors by their proportional eigenvalue. The factors were standardized to unit variance using correlation coefficients to achieve a more balanced ordination. We plotted the locations of males and females and the controls as vectors onto the ordination using the function "envfit" as implemented in vegan 1.17–4 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. 2010).

To quantify niche overlap between the sexes and between individuals and controls we used the Czechanowski index (Feinsinger et al. 1981). This index ranges from 0 (no similarities in resource utilization) to 1 (identical resource utilization). We excluded the parameter "bare ground", as this structure was measured only in <1% of locations. To test whether the observed niche overlap differed from a random pattern we carried out null model analyses with EcoSim 7.72 (Gotelli and Entsminger 2001). EcoSim simulates patterns of niche overlap and compares these randomized results with the observed data matrix. We used the algorithm RA3 (Winemiller and Pianka 1990) to test for non-random niche overlap. In this 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. We defined the relative availability of each resource state using the data of the corresponding control samples. For each data set 30,000 replicates were created in the simulation.

In order to analyse the effect of behaviour on microhabitat utilization, we included "behaviour" (with the factor levels "resting"($N = 172$), "singing" ($N = 132$), "locomotion" ($N = 65$), "cleaning" ($N = 24$) and "feeding"($N = 8$)), "substrate" (with the factor levels "rushes" ($N = 189$), "forbs" ($N = 123$), "grasses" ($N = 56$), "litter" ($N = 34$)) and "sex" ($N = 199$) as explanatory variables and the environmental parameters (i.e. vegetation structure and microclimate) as the response variable in a three-way ANOVA. Mating and oviposition behaviour occurred too scarce to include them in the statistical analyses. In case of significance, we conducted multiple t-tests with Bonferroni correction to find the most important behaviour or substrate type influencing our data. For the vegetation cover, we excluded the factor "substrate". All tests were carried out with "R 2.10.0" (R Development Core Team 2009).

Results

Population size

In total, we obtained 1,246 captures (Table 1). The recapture rate (i.e. the proportion of individuals that were recaptured at least once) was 56.2% with no significant difference between the sexes (Table 1). The best supported model in MARK gave a population size estimate of 552 (±32 SE) females and 452 (±27 SE) males. The model was described by the formula ϕ(T)p(t)pent(t)N(g) (AIC: 4368.43, 40 parameters), i.e. a linearly increasing rate of population decline, temporarily variable capture probabilities and recruitment rates as well as sexual differences in the number of individuals. The four next best fit models included sexual differences in population decline, capture probabilities and/or recruitment and showed only minor differences in population size estimates per sex (Online Resource 1). The part of the study site that was occupied by *C. montanus* had an area of 4,451 m^2, resulting in a population density of 0.23 individuals per m^2 (Fig. 1). The population was spatially subdivided into two main clusters, which were separated by a wet area of higher vegetation. The positions of these clusters remained more or less constant in time. A total of 24 individuals (7.5% of the recaptured individuals) changed between the clusters.

Mobility parameters

The sexes differed not significantly in any measure of mobility (ANOVAs with log-transformed data, n.s.). Most of the adult individuals (56.6%) reached a cumulative distance of ≤20 m (Fig. 2). The maximum value was found in a female, which attained a distance of 104 m. Among males, the maximum cumulative distance moved was 97 m. The maximum distance between two captures of one individual was 75 m, but 80.1% of the individuals

Table 1 Number of marked individuals, recapture events, recaptured individuals and recapture ratio of *Chorthippus montanus* on the study site near Prosterath (Hunsrück, Germany)

	Marked individuals	Recaptures	Recaptured individuals	Recapture ratio (%)
Females	313	392	181	58
Males	256	285	139	54
Total	569	677	320	56

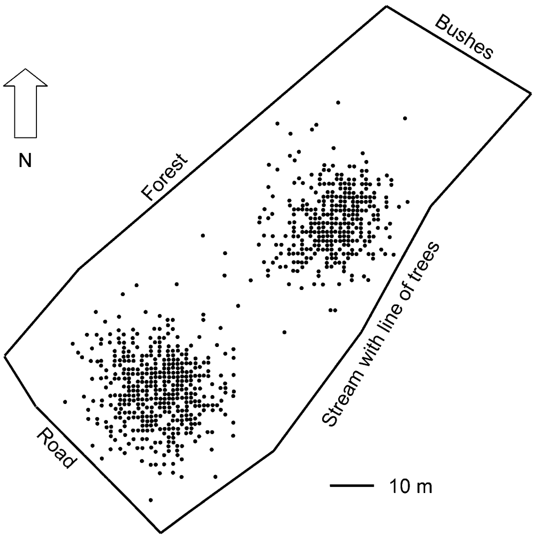

Fig. 1 Outline of the study site with all capture and recapture points of *Chorthippus montanus*

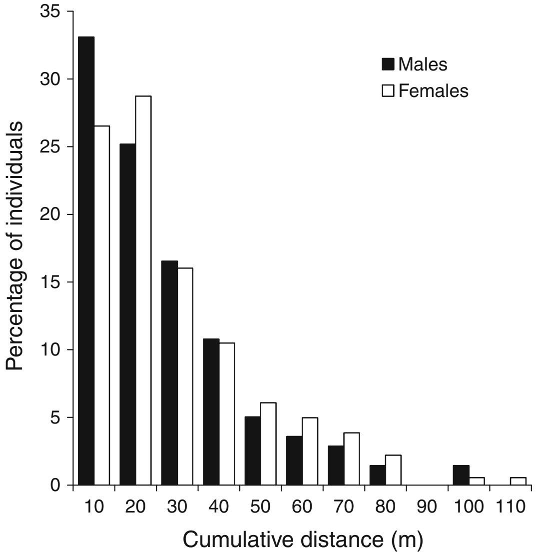

Fig. 2 Cumulative movement distances (i.e. totals of all single distances) of male and female *Chorthippus montanus* measured from 24 July 2009 to 28 September 2009 on a study site near Prosterath (Rhinland-Palatinate, Germany)

remained in a distance <20 m. The maximum movement distances were significantly lower than those inferred from a random data set (ANOVA with Box-Cox-transformed data, $F_{1,638} = 335.4$, $P < 0.0001$; Fig. 3). Concerning the distance per day, most individuals (67.2%) moved ≤ 2 m (mean: 2.51 m ± 0.21 m SE). Only ten individuals (3%) reached distances >10 m per day.

Our curve fitting analysis revealed that the data distribution was best explained by the function Y = A*(EXP(B*X)-EXP(C*X)), with A = −319.62, B = −0.1264 and C = −0.0542 (R^2 = 0.994, Red. $\chi^2 = 9.09$; Fig. 4). Fitting traditional two-parameter models (exponential and power functions) to the data produced substantially worse results. Inserting the population estimate ($\approx$1,000 individuals) in the function, a distance of 120 m would be reached by 1.5 individuals, 130 m by 0.9 individuals and 140 m by 0.5 individuals. The probability that an individual would make it up to a cumulative distance of 200 m was 0.02.

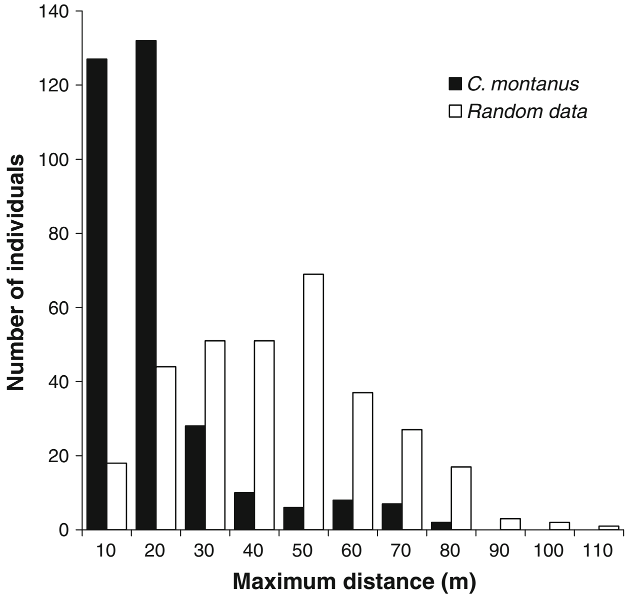

Fig. 3 Maximum movement distances (i.e. maximum distances between two single points of capture) for *Chorthippus montanus* and for a random data set based upon 320 random distances drawn from the complete data set

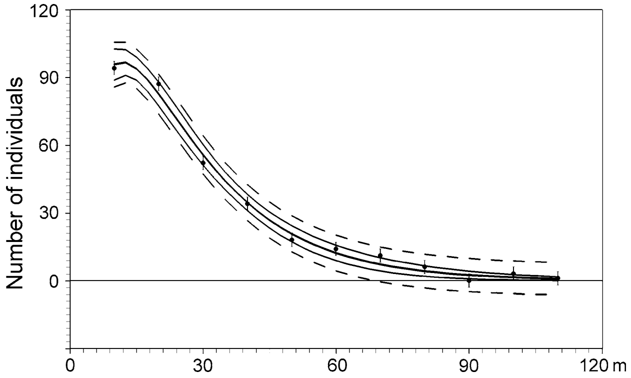

Fig. 4 Best fitting model for the cumulative movement distances of *Chorthippus montanus* (*central line*) with prediction band (*solid lines*) and 95% confidence intervals (*broken lines*). *Black circles* are the measured values, *error bars* are standard errors

Microhabitat analysis

Altogether, 201 microhabitat records per sex were included in the analysis (i.e. 16.8 records per day). We found no significant differences in habitat utilization between the

Table 2 Results of three-way ANOVAs on significant effects of sex, behaviour and substrate on the microhabitat parameters measured at the direct location of *Chorthippus montanus* individuals

Parameters	Sex			Behaviour			Substrate		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Perch height	1,371	<0.01	0.925	4,371	2.94	0.020*	3,371	16.74	<0.001*
Temperature	1,391	0.09	0.759	4,391	5.03	<0.001*	5,391	6.12	<0.001*
Radiation	1,371	1.17	0.279	4,371	0.77	0.542	3,371	2.07	0.104
Vegetation height	1,369	0.14	0.713	1,369	1.14	0.338	3,369	12.10	<0.001*
Rushes	1,392	0.3	0.582	4,392	1.57	0.182	–	–	–
Grasses	1,392	0.59	0.442	4,392	1.82	0.125	–	–	–
Forbs	1,392	0.48	0.487	4,392	0.78	0.539	–	–	–
Litter	1,394	<0.01	1.000	4,394	1.68	0.1532	–	–	–

No significant interactions occurred

* Marks significant *P* values

Table 3 Results of Fisher's *F* tests for differences in the variance of microhabitat parameters between the sexes of *Chorthippus montanus*

Parameters	*df*	*F*	*P*
Exact location	200	0.83	0.192
Temperature	199	0.93	0.588
Radiation	200	0.90	0.464
Vegetation height	199	0.97	0.804
Rushes	199	0.98	0.906
Grasses	199	1.04	0.782
Forbs	199	0.94	0.658
Litter	199	0.92	0.550

sexes for substrate (χ^2 cross table test; $\chi^2 = 3.35$, $df = 3$, $P = 0.34$) or any metric variable (Table 2). The variances associated with the means did also not differ significantly among sexes (Table 3). The locations of individuals were significantly warmer and had significantly greater radiation than the corresponding control measures (paired *t* tests; Table 4; Fig. 5). For the other variables, no significant differences were found. The variances associated with the means of nearly all parameters did not differ significantly between the insects' locations and the controls (*F* tests; Table 4). Litter cover was the only parameter, where significant differences in the variances were found ($s^2_{\text{insect}} = 94.7$, $s^2_{\text{control}} = 70.2$).

The first function of the principal component analysis explained 26.6% of the variance, the second one 19.4%. The first axis was mainly explained by vegetation height (score: 2.15) and grass cover (score −2.29), the second by radiation (score: 2.3) and forb cover (score: 2.1). Both the locations of the individuals and the control measures correlated significantly with the PCA functions 1 and 2 (environmental fitting, $P = 0.022$). The locations of the individuals correlated positively with temperature and radiation and negatively with cover of rushes, whereas the control measures showed negative correlations with the individuals (Fig. 6).

Niche overlap

Generally, the niche overlap between the sexes was higher than expected by chance. For the parameters substrate, perch height, temperature and radiation, the observed niche overlaps were significantly higher than the simulated mean niche overlaps (Table 5). The niche overlaps for vegetation height and cover of rushes, grasses, forb and litter did not differ significantly from a random pattern (Table 5). The niche overlap between the insects' locations and the associated control sites was generally lower than expected by chance. These differences were significant for nearly all microhabitat parameters, except for temperature (Table 6).

Analysis of behaviour and substrate

A three-way ANOVA revealed that temperatures differed significantly among behaviour types and substrates (Table 2). There was a tendency that temperatures were significantly lower (24.6°C ± 0.42 SE) during resting behaviour than when the insects were singing (26.1°C ± 0.38 SE; pairwise t-test with Bonferroni correction, $P = 0.053$). For grasshoppers perching on litter, the recorded temperatures were significantly higher (27.7°C ± 1.04 SE) than for individuals resting on grasses (24.8°C ± 0.65 SE; pairwise t-test with Bonferroni correction, $P = 0.021$) or rushes (24.5°C ± 0.34 SE; pairwise *t* test with Bonferroni correction, $P < 0.001$). Vegetation height (45.40 cm ± 1.01 SE) and perch height (19.14 cm ± 0.58 SE) varied also significantly among different substrates (Table 2). Individuals resting on rushes were found in higher vegetation (49.2 cm ± 1.42 SE) than individuals perching on grasses (32.8 cm ± 2.76 SE) or

Table 4 Arithmetic means and standard errors for environmental parameters measured at the insects' locations and the corresponding control measures; results of paired *t* tests and *F* tests for differences in the variance between the insects' locations and the corresponding control measures

Parameters	Grasshoppers' locations	Control samples	Paired *t* test			*F* test		
			t	*df*	*P*	*F*	*df*	*P*
Temperature	25.22 ± 0.25°C	24.28 ± 0.25°C	5.98	399	<0.001*	1.02	400	0.815
Radiation	60,346 ± 1,558 Lux	55,394 ± 1,635 Lux	4.24	401	<0.001*	0.91	401	0.331
Vegetation height	45.40 ± 1.01 cm	43.99 ± 0.97 cm	1.28	397	0.201	1.08	398	0.451
Rushes	25.51 ± 1.04%	27.16 ± 1.09%	1.48	399	0.139	0.91	399	0.352
Grasses	38.35 ± 1.17%	38.45 ± 1.22%	0	399	1.000	0.92	399	0.396
Forbs	42.84 ± 1.08%	42.77 ± 1.01%	0.18	399	0.859	1.13	399	0.215
Litter	11.02 ± 0.49%	10.07 ± 0.42%	1.74	399	0.082	1.35	399	0.003*

* Marks significant *P* values

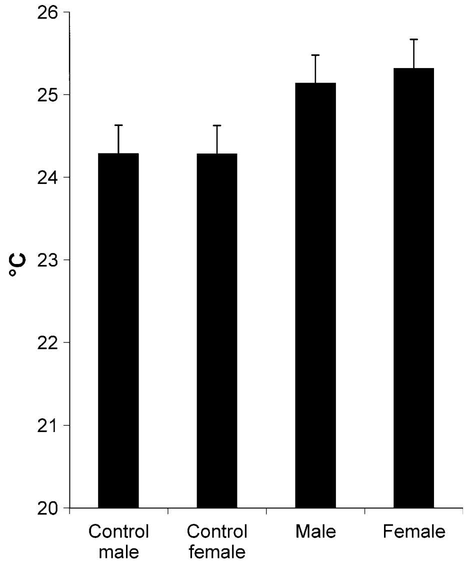

Fig. 5 Average temperature at the locations of male and female *Chorthippus montanus* individuals and their associated controls (measured in a distance of 1 m). Locations of individuals were significantly warmer than control measures ($P < 0.001$)

litter (34.6 cm ± 3.47 SE; pairwise t-tests with Bonferroni correction, $P < 0.002$). A similar pattern was found for perch height. Insects found on rushes were resting higher above the ground (22.5 cm ± 0.86 SE) than on forbs (18.2 cm ± 0.96 SE), grasses (11.9 cm ± 1.05 SE) and litter (13.5 cm ± 1.75 SE; pairwise *t* tests with Bonferroni correction, $P < 0.004$).

Discussion

The population studied had an estimated size of about 1,000 individuals, which is among the largest reported for this species (Radlmair 2003). Hence, it is likely that the habitat had a high quality. Most individuals remained in a distance of less than 20 m from the point of first catch, supporting the hypothesis that most Orthoptera are rather sedentary (Ingrisch and Köhler 1998b). The main factors influencing the microhabitat preferences of *C. montanus* on the study site were temperature and radiation, which is typical for many Acrididae (Uvarov 1977). Although many Orthoptera show intersexual differences in their habitat preferences (Hochkirch et al. 2007b) and mobility (Ingrisch and Köhler 1998b), this was not confirmed in *C. montanus*.

Mobility

Since *C. montanus* is flightless (except for the rare macropterous morph), the movement distances were rather low, with an estimated probability of only 0.5 individuals reaching a cumulative distance of 140 m and a recorded maximum distance of 75 m between two catches. As the complete study site was searched for individuals, but only few specimens were found outside the habitat, it is rather unlikely that individuals emigrated (except for macropterous individuals). The mean daily movement was comparable to other flightless Orthoptera (e.g. Mason et al. 1995; Kindvall 1999; Gardiner and Hill 2004, Diekötter et al. 2005, López et al. 2007). In contrast, alate Orthoptera species usually move larger distances (e.g. Hein et al. 2003; Maes et al. 2006). However, it should be noted that we only marked adult individuals. This was necessary as it is virtually impossible to mark nymphs permanently, because the markings are lost with each moult (Diekötter et al. 2005). Second, it is not possible to distinguish all nymphal instars of *C. montanus* from the sibling species *Chorthippus parallelus* (Oschmann 1969). Hence, mobility during the nymphal stage remains unknown. Nevertheless, it is likely that nymphs move only little as they often stay close to the place of oviposition for feeding (Alcock 1972). Clumped dispersion patterns are, therefore, typical for many Orthoptera species (Gröning et al. 2007b).

Fig. 6 First two axes of a principal component analysis (PCA) of the environmental parameters (microclimate and vegetation) at the exact location of the individuals (46% of the total variance is explained). The factors were standardized to unit variance using correlation coefficients to achieve a more balanced ordination. The locations of insects and controls were fitted as vectors onto the ordination using the environmental fitting function (envfit) in vegan 1.17–4 for R

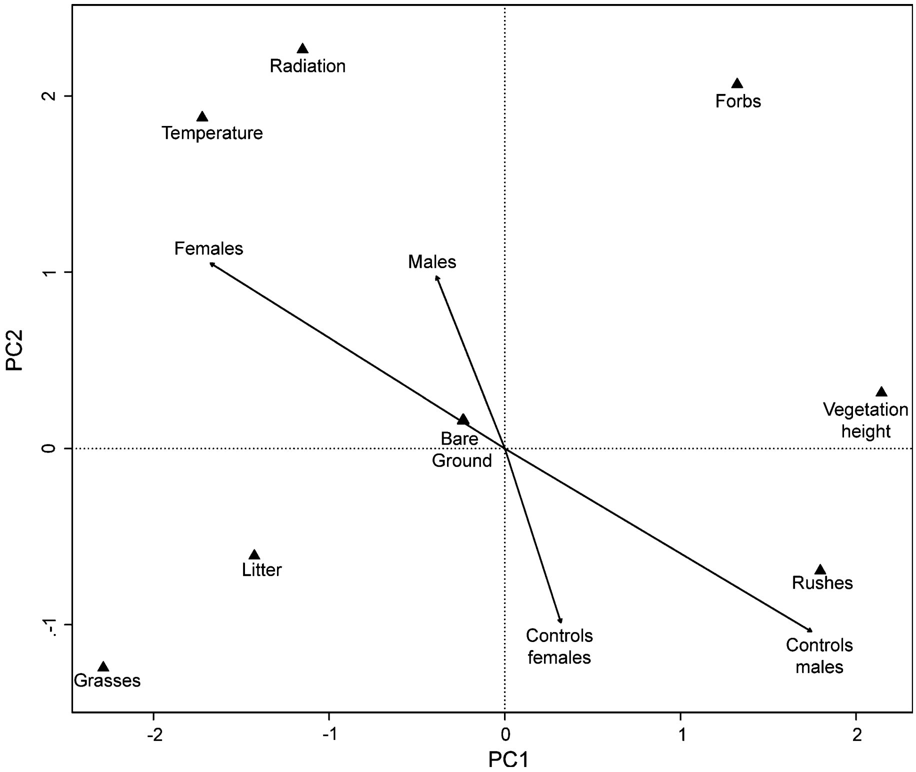

Table 5 Niche overlap in microhabitat utilization between males and females of *Chorthippus montanus* calculated with Ecosim 7.72 using 30,000 replicates per simulation

Parameters	Observed mean		Simulated mean	*P*
Substrate	0.94	>	0.70	0.040*
Perch height	0.92	>	0.54	<0.001*
Temperature	0.77	>	0.55	<0.001*
Radiation	0.78	>	0.69	0.022*
Vegetation height	0.82	>	0.75	0.065
Rushes	0.81	>	0.79	0.271
Grasses	0.76	>	0.76	0.487
Forbs	0.67	>	0.67	0.471
Litter	0.55	<	0.61	0.231

* Marks significant *P* values

Table 6 Niche overlap between occupied microhabitats of *Chorthippus montanus* and unoccupied control sites calculated with Ecosim 7.72 using 30,000 replicates per simulation

Parameters	Observed mean		Simulated mean	*P*
Temperature	0.66	<	0.70	0.095
Radiation	0.76	<	0.81	<0.001*
Vegetation height	0.70	<	0.76	0.002*
Rushes	0.89	<	0.92	0.004*
Grasses	0.91	<	0.93	<0.001*
Forbs	0.87	<	0.91	0.006*
Litter	0.71	<	0.78	<0.001*

* Marks significant *P* values

We found no significant difference in the movement distances between male and female individuals. This result is rather surprising as the mobility of male grasshoppers is usually higher than in females (Mason et al. 1995; Maes et al. 2006; Walters et al. 2006; López et al. 2007). The main reason for this is that male grasshoppers actively search for females, while females invest more time in feeding (Hochkirch et al. 2007b). Hence, movement behaviour is influenced by the availability of resources, such as food, oviposition sites or mates. If habitat quality and resource availability are high (and competition is low), there is no need for grasshoppers to move. In case of low habitat quality or high competition, the motivation for movement should be stronger (Gardiner and Hill 2004). However, individuals might stop or return when reaching unsuitable habitat (Kindvall 1999). Hence, the habitat size might also influence mobility, but mainly if competition is strong. The low movement rates of *C. montanus* compared to random data indicate that habitat quality (i.e. resource availability) on the study site was high and competition was low. As only few individuals were found outside the damp area of the study site, *C. montanus* is unlikely to leave its habitat and colonize new habitat patches. The only possible mechanism to reach new habitats is the rare macropterous morph, which is also found in other Orthoptera species and is able to cross larger distances by flight (Hochkirch and Damerau 2009). The importance of this morph for *C. montanus* still remains to be studied.

Population size

Although a population size of ca. 1.000 individuals seems to be rather large for this species (Radlmair 2003), we suggest that most reported population sizes for *C. montanus* are underestimated. Most estimates are not based on mark-recapture studies, but simply on single inspections. As we achieved a maximum of 70 individuals per day, it is reasonable to assume that population sizes are difficult to assess by single counts. Nevertheless, the population sizes of *C. montanus* are probably often smaller than in other Orthoptera as the species has a very narrow niche and is only found in permanently damp (but not too wet) habitats (Lorz and Clausnitzer 1988). These habitat patches are usually small and naturally fragmented. In contrast, less specialized grassland Orthoptera (as for example *C. parallelus*, *Metrioptera roeselii*) may have highly interconnected populations that are linked by fringes and other types of corridors, forming extremely large populations (Holzhauer et al. 2009). The combination of small population sizes, low mobility and strong habitat fragmentation makes *C. montanus* particularly vulnerable to land use changes.

Microhabitat preferences

In contrast to other studies on Orthoptera (e.g. Hochkirch et al. 2000, 2007b; Gröning et al. 2007b), we found no intersexual differences in microhabitat utilization. Niche overlap between the sexes was greater than expected by chance, while niche overlap between the insects locations and the controls was smaller than expected by chance. The latter confirms that grasshoppers perform an active habitat choice (Whitman 1987; Gröning et al. 2007a). Both sexes preferred patches with high temperatures and radiation. This is rather typical for grasshopper species, most of which prefer temperatures of 30–42°C (Uvarov 1977, Ingrisch and Köhler 1998b). However, it is rather surprising that even species confined to damp, cool habitats follow this pattern. It seems that the hygrophilous behaviour of *C. montanus* is mainly driven by water requirements of the egg stage (Ingrisch 1983a). Nymphs and adults appear to prefer warmer and brighter sites in order to gain enough energy for development and activities. The latter is confirmed by the warmer temperatures recorded during singing behaviour compared to resting individuals. The results of the PCA are amazingly similar to those found by Gröning et al. (2007b) for two other hygrophilous grasshopper species, *Tetrix ceperoi* and *Tetrix subulata*. Thus, hygrophilous grasshoppers might be particularly dependent on warm patches in the cool habitat in order to reproduce successfully.

It is surprising that *C. montanus* does not exhibit a strong preference for a special vegetation structure, which is typical for many other Orthoptera species (Sänger 1977; Ingrisch and Köhler 1998b; Hochkirch and Adorf 2007). This might be influenced by the rather homogeneous vegetation of the study site, where patches with suitable vegetation structure do not seem to be limited. Since grasses are abundant in the habitat, food is not limited for this graminivorous grasshopper species (Ingrisch and Köhler 1998b). As many ecological phenomena are scale dependent (Levin 1992), one might expect that on a coarser scale other factors (particularly soil moisture and vegetation density) play a more important role for the distribution of *C. montanus* (but see Gröning et al. 2007b). However, on a micro-scale Water-Meadow Grasshoppers seem to be mainly influenced by microclimatic factors. These results are in good accordance with those of Langmaack and Schrader (1997), who found a preference for median vegetation density in this species and a narrow niche compared with two other grasshopper species. A dense or high vegetation might negatively influence the microclimate on a meadow. Therefore, the Water-Meadow Grasshopper usually disappears if a meadow or pasture is abandoned and vegetation structure becomes to dense and high (Detzel 1998). Hence, methods of open-land management, such as mowing and grazing, are vital for the survival of *C. montanus* populations.

The cool mesoclimate of wet habitats compared to dryer ones might explain why nymphs of *C. montanus* generally hatch approximately a month later than those of its sibling species *C. parallelus* (Ingrisch and Köhler 1998b; Hochkirch and Lemke 2011). During development nymphs are known to become more and more thermophilous and prefer warm patches with a low humidity (Ingrisch 1980). Water deficiency during hibernation can hamper or delay their development (Ingrisch 1983b) resulting in extinction of the population through inefficient reproduction in the long run. We found nymphs of *C. montanus* until mid October, indicating that even in viable populations some individuals are not able to complete their life cycle. High and dense vegetation (as found in fallow land) promotes colder temperatures and thus might increase the number of such individuals. A dense vegetation cover also reduces the number of oviposition sites and might also negatively influence the mobility. For these reasons draining and abandonment are the major threats for *C. montanus*.

Conservation implications

Wetlands are globally threatened by a number of factors, including agricultural intensification, draining, water regulation, dams, eutrophication, chemical pollution and invasive species (Brinson and Malvárez 2002). One recent factor threatening wetlands in Central Europe is abandonment. During our search for study sites, we used information on the occurrence of *C. montanus* obtained in the 1980s and 1990s (for 22 sites). Four of these former grasslands were now fallow land and the populations of the Water-Meadow Grasshopper on these sites were not rediscovered. This process is mainly caused by the low profit obtained in extensively used grassland. For species with narrow niches and a low mobility, such as *C. montanus*, habitat changes often lead to regional extinctions and increase the fragmentation of the remaining populations. In order to preserve *C. montanus* it is necessary to maintain the current management of sites where it still occurs and to implement extensive grassland management at sites where it declines. As the number of populations is still declining, habitat restoration is needed in order to reconnect wetland habitats (Exeler et al. 2009). Our microhabitat data can help to make management recommendations for this endangered species.

In contrast to other endangered wetland Orthoptera, such as *Stethophyma grossum*, which is a strong flyer and mainly needs seasonal flooding of the eggs (Ingrisch 1983b; Lorz and Clausnitzer 1988; Fricke and von Nordheim 1992), *C. montanus* requires constantly wet habitats. A recent search for both species in an adjacent valley to our study site revealed 65 populations of *S. grossum*, but none at all for *C. montanus* (although historical records of the latter species exist, Erchinger personal communication). This result supports the conclusion that *C. montanus* is one of the most specialized wetland species among Central European Orthoptera. Hence, a second current threat for *C. montanus* is still draining (Langmaack and Schrader 1997), which is often accompanied by an intensification of the agricultural practices. Changes in soil moisture are fatal to the eggs of *C. montanus*, which are particularly sensitive to desiccation (Ingrisch 1983a). They also lead to secondary changes in the vegetation and the local microclimate. Populations of specialised wetland species are likely to become extinct due to drainage. Thus, avoiding draining or restoring the natural water regime is an urgent measure in order to preserve threatened invertebrate species. Extensive agricultural practices are strongly associated with undrained wetlands.

A number of studies have dealt with optimal management practices of grasslands for preserving Orthoptera. Mowing is crucial in order to maintain a medium vegetation height and density, but the management should not be to intensive. Some authors have recommended that mowing should take place only once or twice per year, either before the nymphs are hatching (before mid May, Fricke and von Nordheim 1992) or after reproduction has been more or less completed (after mid September, Gardiner and Hassal 2009; Oppermann 1987; Fricke and von Nordheim 1992). Alternatively, rotational mowing has been proposed if a cut during summer cannot be avoided (Gardiner and Hassal 2009). Other strategies to retain viable populations are to mow margins of 2–5 m only occasionally or leave parts of the hay at the sites to avoid loss of insects with each cut (Fricke and von Nordheim 1992). On pastures, a maximum continuous stocking rate of one cattle per ha has been recommended (Fricke and von Nordheim 1992). Driving the cattle among different pastures can help to reduce ongoing pressure on the existing population, but only if the cattle density is low. In order to create suitable habitat for as many species as possible, large grassland complexes should be managed heterogeneously to create a mosaic of different vegetation structures and microclimates with margins and corridors to connect them (Fricke and von Nordheim 1992; Oppermann 1987). These types of management would not only promote Orthoptera but also other wetland species (Brinson and Malvárez 2002).

Habitat fragmentation is a major problem for many species (Fahrig 2003) and particularly for flightless insects such as *C. montanus*. Currently, new pressures on wetland habitats arise due to changes in agricultural policies. The increasing cultivation of biofuels accelerates habitat loss also for wetland species. During the study year, we observed that a former wet meadow was converted into a cornfield. Furthermore, it is likely that wetland species are affected by climate change, which might increase the occurrence of drought periods in Central Europe. This would be particularly harmful to *C. montanus*. Among the historical records of *C. montanus* all (three) populations that formerly occurred at altitudes <400 m a.s.l. had vanished. Altogether, we rediscovered only two-third of the known populations, suggesting that population fragmentation still increases for this species. In order to assess the current population fragmentation and the dispersal capacity, population genetic analyses are needed (Johannesen et al. 1999). Indeed, results from mark-recapture studies are often in strong contrast to the results obtained by genetic studies. Johannesen et al. (1999) found a high gene flow between populations of the grasshopper *Stenobothrus lineatus* despite a low mobility measured in a mark-recapture study. This suggests that either dispersal is under-estimated in field studies as the probability to find individuals decreases exponentially with the distance (Hochkirch and Damerau 2009) or that the genetic structure of populations is stronger influenced by historical events than by ongoing gene flow (Exeler et al. 2010). However, based upon the existing data it seems likely that populations of *C. montanus* are strongly fragmented as has been shown in other flightless Orthoptera species (Witzenberger and Hochkirch 2008).

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