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ORIGINAL ARTICLE

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Habitat preferences of an endangered insect species, Cepero's ground-hopper (*Tetrix ceperoi*)

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Abstract Preventing the global decline in biodiversity is a major task for conservation biologists. Although habitat loss has been identified as a key factor driving extinction processes, our knowledge on the habitat requirements of many endangered species, particularly invertebrates, is still sparse. We present a feasible method to study the microhabitat preferences of insect species. In Central Europe, the endangered Cepero's ground-hopper, *Tetrix ceperoi*, is believed to have its only remaining natural habitats in dune slacks of the Wadden Sea Islands. Our results suggest that this species performs an active habitat choice of damp, bare patches with high temperatures. While ponds and fens in dune slacks provide large areas of damp bare ground and algal mats, grasslands, degraded dune slacks and the transitional zone between salt marsh and dunes are less suited as habitats. The major threat for *T. ceperoi* is found in the succession of its pioneer habitats due to the reduced natural dynamics. In industrialized countries, pioneer habitats and species are threatened substantially by coastal protection and floodplain regulation. This is only compensated in part by anthropogenic creation of secondary habitats, such as different kinds of pits or coal heaps. Nevertheless, there is a strong need for restoration of dynamic habitats by floodplain revitalization and dune slack restoration.

Keywords Dune slacks · Extinction · Floodplains · Insect conservation · Restoration

Introduction

The global loss of biodiversity is a major problem of modern times (Wilson 1988). Many species are threatened by human activities, and are likely to disappear without immediate site-specific action (Ricketts et al. 2005). The main factors driving extinction processes are habitat loss, fragmentation, invasions, exploitation and climate change (Primack 2002; Tscharntke et al. 2002; Fahrig 2003; Thomas et al. 2004; Clavero and García-Berthou 2005). While complete extinctions have been reported mainly from biodiversity hotspots (Ricketts et al. 2005), regional decline of species richness is known from all over the world (e.g., Dennis and Shreeve 2003; Haig et al. 2005).

In order to perform conservation measures and design management plans, ecological knowledge of endangered species is of crucial importance (Primack 2002; Samways 2005). Although habitat loss is believed to be the main threatening factor for most taxa, the habitat requirements of many insect species are insufficiently documented, while habitat preferences of endangered vertebrates are well understood (Dunn 2005; Samways 2005). Orthoptera have become an important group for environmental impact assessments and bioindication in Central Europe (Maas et al. 2002; Szövényi 2002). In comparison with other insects, the decline of most Orthoptera species in Germany is fairly well documented (Ingrisch and Köhler 1998; Maas et al. 2002). The key factors for the occurrence of most Orthoptera species are found in special vegetation structures and microclimates (Sänger 1977; Ingrisch 1980). Grasshoppers are believed to perform an active habitat choice (Whitman 1987) and often have special behavioral adaptations to small habitat features, such as oviposition sites, feeding habitats or courtship sites (Hochkirch et al. 2000).

Cepero's ground-hopper, *Tetrix ceperoi* (Bolivar, 1887), is one of two cases of Orthoptera species, in which the red list status in Germany is unknown (category "data deficient", Maas et al. 2002). In Lower Saxony, it has been classified as endangered (Grein 2005). It is a pioneer species of dynamic floodplains and coastal dune systems, which belong to the most threatened habitat types in Central Europe. Since riverine ecosystems have

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been heavily degraded, moist dune slacks on the East Frisian Islands (Lower Saxony) seem to be the only remaining natural habitats in Germany (Gröning et al. 2005). Here, we present an analysis of the habitat preferences of *T. ceperoi*. First, we tested the hypothesis that the species performs an active habitat choice by comparing occupied microhabitats with the surrounding non-occupied environment. We used the differences between variances of environmental parameters measured at the insects' locations and at a corresponding control as indicators of niche breadth. Smaller variances at the insects' locations indicate a narrow niche compared to the surrounding environment. Second, we tested the quality of the microhabitat preferences by comparing the average values of vegetation structure and microclimate of the ground-hoppers' location with the control. Third, we compared populations of different habitat types for differences in their microhabitat choice and tested these habitat types for suitability.

Methods

The study object

Tetrix ceperoi is a West-Mediterranean species, which reaches the north-eastern edge of its range in Central Europe (Kleukers et al. 1997). It is usually restricted to damp, warm habitats, such as dune slacks, sand and clay pits, coal heaps, drainage ditches or heath ponds (Ingrisch et al. 1988; Marshall and Haes 1988; Krüner 1993; Detzel 1998; Gröning et al. 2005). On the German mainland, *T. ceperoi* is rare and only found in anthropogenic habitats (Ingrisch et al. 1988; Kleukers et al. 1997; Detzel 1998), whereas on the East Frisian Islands the species occurs in virtually all damp places, including both primary and secondary habitat types (Gröning et al. 2005). As most Tetrigidae, *T. ceperoi* is terricolous and feeds on a variety of algae, mosses, small plants and detritus (Paranjape et al. 1987; Hochkirch et al. 2000; Bastow et al. 2002). Adults of this species reproduce in May and June and are fully winged (Kleukers et al. 1997).

Data collection

The data were obtained on the isle of Langeoog (ca. 20 km^2), which is one of the East Frisian Islands and part of the national park "Niedersächsisches Wattenmeer". Prior to the fieldwork, the occurrence of *Tetrix* species on the isle was mapped in order to locate study sites with sufficiently high abundances (Gröning et al. 2005). The species was recorded from 19 sites, 8 of which were chosen for the data collection (Table 1). The fieldwork was carried out during the reproductive period of *T. ceperoi* from 7 May to 26 June 2004. Other Tetrigidae (potential competitors) were virtually missing on Langeoog and absent from all of our study sites.

For the analysis of microhabitat preferences, data were obtained at the exact location of randomly chosen individuals during the time of their activity (between 1100 and 1700 hours). Recorded data included date, site, time, weather, sex and color morph. Radiation was measured using a luxmeter, Elvos LM 1010. Temperature measurements were made with a digital infrared thermometer (Raytek MiniTemp). Relative humidity was measured with a digital thermohygrometer (Lutron HAT 3004) 1 cm above the ground. The vegetation structure was estimated in a circle of 30 cm diameter surrounding the insect, including the cover of bare ground and algal mats, grasses, forbs and dwarf shrubs, litter and mosses, as well as the maximum vegetation height. Since the population sizes at our study sites were sufficiently large, the risk of pseudoreplication was low. In addition to the individual data, a control sample of all factors was measured at a distance of 1 m from the location (in a random direction). We chose this distance for two reasons. First, the control is easily attainable for the insects, as their mean jump distance is ca. 30 cm (Hochkirch et al. 2002). Second, heavy changes in vegetation structure and microclimate usually occur on this micro-scale, allowing us to test for active habitat choice. For analyzing the suitability of different habitat types, the study sites were assigned to the following habitat types: degraded dune slacks, fens, ephemeral ponds, transitional zone between dunes and salt marsh, and moist grassland (Table 1).

Table 1 Study sites, geographical position (GPS), number of records and habitat type

Site	GPS	Records (*n*)	Habitat type
L1	53°45.238′N, 7°30.916′E	174	Degraded dune slack
L2	53°45.023′N, 7°30.109′E	104	Ephemeral pond in dune slack
L3	53°44.978′N, 7°30.184′E	54	Fen in dune slack
L4	53°45.033′N, 7°33.206′E	91	Transitional zone between salt marsh and dunes
L5	53°45.021′N, 7°33.328′E	25	Transitional zone between salt marsh and dunes
L9	53°45.002′N, 7°36.875′E	15	Moist grassland
L12	53°45.138′N, 7°32.981′E	10	Moist grassland
L13	53°45.264′N, 7°33.053′E	20	Moist grassland

Statistical analyses

To compare the locations of the insects with the control samples, we carried out paired *t* tests. We used Fisher's *F* test to compare the variances associated with the means of the insects' location and the control sample (Crawley 2005). In order to identify correlations between the different environmental factors and the main correlation of the locations of *T. ceperoi*, we performed a standardized principal component analysis (PCA), using the function "rda" of the community ecology package vegan 1.6–10 for R (Oksanen et al. 2005). The function 'rda' uses scaling of the factors by the proportional eigenvalue, which is particularly useful for our data set with its rather variable scales (lux, °C, cm, % cover). The factors were standardized to unit variance using correlation coefficients to achieve a more balanced ordination. The *T. ceperoi* locations were fitted as vector onto the ordination using the function 'envfit' (Oksanen et al. 2005).

To analyze the suitability of different habitat types, we performed two-way ANOVAs, including location (species vs control) and habitat type as explanatory variables and the vegetation data as response variable. Pairwise *t* tests with Bonferroni correction were used to identify the differing habitat types. If necessary, data were boxcox-transformed using Venables and Ripley's MASS library for R (Venables and Ripley 2002). All statistical analyses were carried out with R 2.1.1 (R Development Core Team 2005).

Results

Microhabitat preferences and niche breadth

A total of 493 individual microhabitat records was obtained (Table 1). The analyses of both biotic and abiotic factors revealed significant differences between the locations of *T. ceperoi* and the associated control samples at the 1-m distance (Table 2). While temperature, radiation and cover of bare ground and algae were significantly higher at the locations of *T. ceperoi*, vegetation height and cover of grasses, forbs and dwarf shrubs, mosses and litter were higher at the controls (Table 2, Fig. 1). No significant difference was found for relative humidity. The variances of temperature, radiation, vegetation height, cover of mosses, grasses, forbs and dwarf shrubs and litter were significantly smaller at the location of the insects than at the control samples (Table 2). No significant difference in variance was found for the factors relative humidity and cover of bare ground and algal mats. A plot of the first two axes of the PCA (43.4% of the total variance) and the vector of *T. ceperoi* locations is given in Fig. 2. It is apparent that, in a multidimensional framework, the factors of bare ground, temperature and radiation, are positively correlated with the *T. ceperoi* locations, whereas grass cover, vegetation height and relative humidity are negatively correlated.

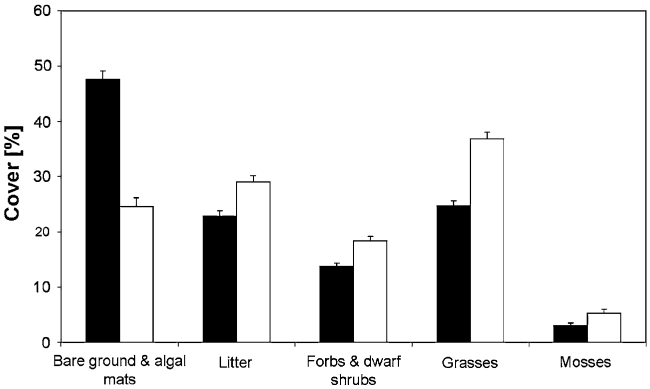

Fig. 1 Vegetation cover at the location of *Tetrix ceperoi* (*black columns*) and at the control samples at 1-m distance (*white columns*) illustrating the preference for bare patches. *Error bars* are standard errors

Table 2 Results of the paired *t* tests and Fisher's *F* tests between the location of *Tetrix ceperoi* and the control sample ($df = 492$)

Factor	Paired *t* tests		Fishers *F* tests			
	t	P	V_{TC}	V_{CO}	F	P
Temperature	8.95	< 0.001	36.80	45.88	0.80	0.014
Radiation	10.33	< 0.001	1.13E + 09	1.36E + 09	0.83	0.040
Relative humidity	−0.86	0.388	39.48	90.54	1.03	0.720
Vegetation height	−7.48	< 0.001	222.24	384.51	0.58	< 0.001
Vegetation cover						
Mosses	−3.62	< 0.001	112.29	276.91	0.41	< 0.001
Bare ground/algae	13.39	< 0.001	1204.73	1180.42	1.02	0.821
Grasses	−11.00	< 0.001	432.63	736.09	0.59	< 0.001
Forbs/dwarf shrubs	−5.66	< 0.001	185.18	335.37	0.55	< 0.001
Litter	−5.45	< 0.001	488.48	633.60	0.77	0.004

Positive *t* values indicate a higher value at the location than at the control and vice versa. Note that in most cases V_{TC} (variance at the location of *T. ceperoi*) is significantly smaller than V_{CO} (variance at the corresponding control), indicating a narrower niche breadth of the insect compared to the control sample

Comparison of habitat types

The two-way ANOVA revealed significant differences between the five habitat types for all vegetation parameters (Table 3). The cover of bare ground and algal mats was significantly smaller in moist grasslands than in any other habitat type (pairwise *t* tests with Bonferroni correction: $\lambda = 0.17$, $P < 0.006$). The vegetation was significantly higher in the degraded dune slack (L1) than in all other habitat types (pairwise *t* tests with Bonferroni correction, $\lambda = 0.32$, $P < 0.048$). Moreover, vegetation height was significantly smaller in the ephemeral pond (L2) than in the transitional zones between dunes and salt marsh (L4, pairwise *t* tests with Bonferroni correction: $\lambda = 0.32$, $P < 0.001$). In the fen (L2) and the ephemeral pond (L3) mosses were significantly more abundant and the grass cover significantly smaller than in all other habitat types (pairwise *t* tests with Bonferroni correction: mosses: $\lambda = -0.50$, $P < 0.001$; grasses: $\lambda = 0.40$, $P < 0.001$). Forbs and dwarf shrubs showed a significantly higher abundance at the ephemeral pond and in the fen than in any of the other habitat types (pairwise *t* tests with Bonferroni correction: $\lambda = 0.28$, $P < 0.001$). The cover of litter was significantly smaller in the fen than in any other habitat type, and it was also smaller in the ephemeral pond than in the dune slack, grasslands or transitional zone (pairwise *t* tests with Bonferroni correction: $\lambda = 0.29$, $P < 0.001$). Altogether, the ephemeral pond and the fen differed in five factors from all other habitat types, while only one parameter (litter) was different between them. The other group of habitat types (grassland, transitional zone between dunes and salt marsh, degraded dune slacks) differed only in one or two parameters from each other.

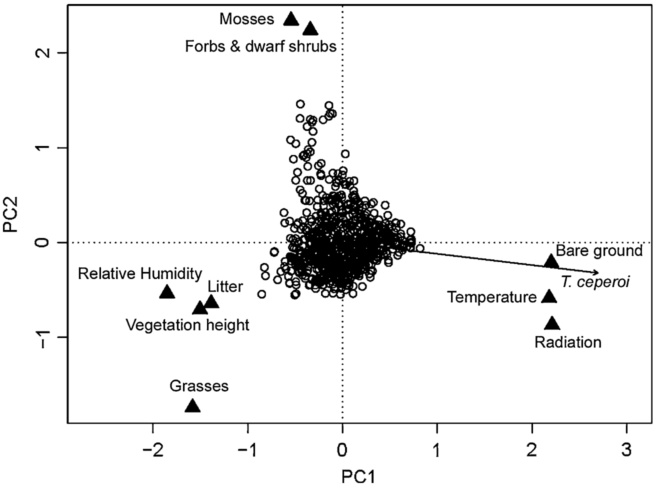

Fig. 2 Plot of the first two principal components of a standardized principal component analysis of the environmental parameters. The factors were standardized to unit variance using correlation coefficients to achieve a more balanced ordination. The *T. ceperoi* locations were fitted as vector onto the ordination, illustrating the strong correlation of the *T. ceperoi* locations with the parameters of bare ground, temperature and radiation

Interactions between habitat type and habitat preference

In four factors (vegetation height, cover of bare ground, forbs/dwarf shrubs, litter), we found a significant interaction between habitat type and microhabitat preference (Table 3). Although there was a general avoidance of high vegetation, this preference for short vegetation was stronger in the grasslands and in the transitional zone than in the other habitat types (Fig. 3). In all habitat types, *T. ceperoi* was found on patches with a higher abundance of bare ground than at the controls. However, the slope between the average cover of bare ground at the insects' location and at the controls was steeper in the grasslands, the transition zone and the degraded dune slack than in habitat types, which had generally a higher abundance of bare ground (ephemeral pond, fen). The avoidance of forbs and dwarf shrubs was stronger at the ephemeral pond, which had a high abundance of *Salix repens*, than in other habitat types. The avoidance of litter was higher in the grasslands, which were characterized by a high amount of litter.

Discussion

Active habitat choice

We present a feasible method to precisely assess the microhabitat preferences of an insect species in its natural habitat, based upon its active habitat choice. Active

Table 3 Results of the two-way ANOVA, using location (species vs control) and habitat type as explanatory variables (residual *df* = 973, λ = transformation exponent)

Factor	λ	Location (*df* = 1)		Habitat type (*df* = 4)		Location:habitat type (*df* = 4)	
		F	*P*	*F*	*P*	*F*	*P*
Vegetation height	0.32	49.68	< 0.001	22.92	< 0.001	5.57	< 0.001
Vegetation cover:							
Bare ground/algae	0.18	171.43	< 0.001	10.11	< 0.001	3.03	0.017
Mosses	–0.50	0.08	0.779	53.54	< 0.001	1.89	0.109
Grasses	0.40	74.69	< 0.001	172.24	< 0.001	2.04	0.086
Forbs/dwarf shrubs	0.28	2.27	0.132	34.58	< 0.001	3.04	0.017
Litter	0.29	13.99	< 0.001	72.43	< 0.001	2.78	0.026

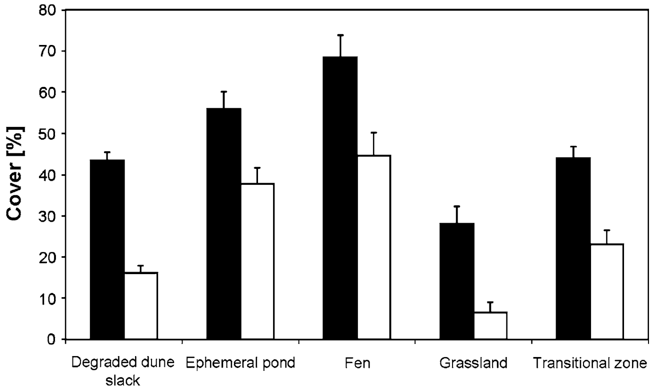

Fig. 3 Cover of bare ground at the locations (*black columns*) and control samples (*white columns*) of different habitat types. The slope between both columns is higher in degraded dune slacks and grasslands than in ephemeral ponds or fens. *Error bars* are standard errors

habitat choice has been documented in a variety of insects, including grasshoppers (Whitman 1987). Their mobility enables them to respond fast to spatial and temporal environmental changes (including social interactions or predator avoidance) and search directly for suitable microhabitats (Anderson et al. 1979; Kindvall et al. 1998). Our results confirm that *T. ceperoi* is choosing its microhabitats actively, since it differed in eight of the ten measured parameters from the environment at 1-m distance. More importantly, the variance of nearly all parameters differed in the expected direction with a higher variability of the control samples. The microhabitat preferences were related to special behaviour types (own data), which illustrates the active habitat choice for special purposes of the life cycle.

Microhabitat preferences of *T. ceperoi*

Detailed analysis of the habitat preferences of *T. ceperoi* have been missing so far. The knowledge on the ecology of the species stems from anecdotal information based upon mapping schemes and faunistic studies (e.g., Marshall and Haes 1988; Detzel 1998). Our results suggest that *T. ceperoi* prefers damp, open patches with warm microclimate and growth of algae. It might be argued that this preference is affected by regional stenotopy, since many species are more specialized at the edge of their range (Kühnelt 1943). However, a preference for bare patches has also been reported from other places throughout the range of *T. ceperoi*, such as Macedonia (Karaman 1960), Serbia (Adamovic 1969), Sardinia (Ingrisch 1983), England (Marshall and Haes 1988), the Netherlands (Kleukers et al. 1997), southern Germany (Ingrisch et al. 1988; Detzel 1998), Switzerland (Thorens and Nadig 1997) and France (Voisin 2003). Detzel (1998) points out that the vegetation cover of its habitat is usually less than 30%. Moreover, most Tetrigidae are terricolous and occur on bare ground (Paranjape et al. 1987), indicating an ancestral evolution of this preference. Bare open patches seem to be essential for the occurrence of *T. ceperoi*, as they provide food (Koen 1996), a preferable microclimate (Chappell and Whitman 1990), courtship sites (Hochkirch et al. 2006), and an oviposition substrate (Detzel 1998). Nevertheless, *T. ceperoi* also utilizes the adjacent patches of dense vegetation to rest and to feed, suggesting that habitat heterogeneity is also of importance for its survival.

Performance of different habitat types

Naturally, *T. ceperoi* seems to be confined to highly dynamic primary habitats with a high proportion of moist and open ground, like floodplains and moist dune slacks. Since virtually all floodplains have been heavily degraded in Germany, the latter habitat types are probably the only remaining natural habitats of *T. ceperoi* in Germany (Gröning et al. 2005). Hence, there is a high responsibility for the conservation and management of its natural habitats by the National Park Administration. The question arises why *T. ceperoi* inhabits a wider range of habitats on Langeoog (e.g., moist grassland) compared to the mainland. Three hypotheses should be investigated in the future to answer this question.

1. The pattern could be influenced by a positive abundance–occupancy relationship (Gaston et al. 2000). Since the number of populations and the abundance in high quality habitats is rather high on Langeoog, the number of occupied (suboptimal) habitats is also higher.
2. Another factor for its frequent occurrence on Langeoog might be competitive release (van Valen 1965). Potential competitors (*T. subulata*) were extremely rare on Langeoog (Gröning et al. 2005). Adamovic (1969) has pointed out that other Tetrigidae were rare or missing on sites where he found *T. ceperoi*. Own experimental data suggest that reproductive interference between *T. subulata* and *T. ceperoi* might hamper their coexistence. In the presence of heterospecifics, the reproductive success of *T. ceperoi* was significantly reduced, since *T. ceperoi* males preferably attempt to mate with *T. subulata* females.

3 The special oceanic climate might provide better microclimatic conditions even in habitats which are less suitable on the mainland (e.g., moist grassland). Although the temperatures are generally lower during the period of activity, the number of sunshine hours is higher on the islands. Solar radiation is the most important heat source for active thermoregulation of grasshoppers (Chappell and Whitman 1990) and this factor might enable them to utilize a broader range of habitats.

Despite the widespread occurrence of *T. ceperoi* on Langeoog, our results indicate that the five habitat types are not of equal quality for the species. The preference for damp open patches is also apparent from the different performances of the habitat types. Habitat types with a greater amount of bare ground and algal mats (dune slacks with fens or ponds) and with strong fluctuations of the water table are suitable, whereas habitats with high and dense vegetation (grasslands, degraded dune slacks, transitional zone between dunes and salt marsh) are only suboptimal. It will be interesting to monitor the abundance of *T. ceperoi* on these study sites in future years. Our data suggest that *T. ceperoi* will disappear from the densely vegetated sites unless bare patches are generated either naturally or artificially.

Management suggestions for the conservation of *T. ceperoi*

Although some of the primary habitats of *T. ceperoi* are still present on the islands, wet dune slack ecosystems are highly threatened by drainage and the lowering of water tables due to the high water demands for tourism (Petersen 1999). Moreover, the natural dynamics of these habitats is strongly restricted by means of coastal protection. In combination with increased eutrophication, these processes accelerate succession towards species-poor shrub communities. Several management techniques have been proposed for preserving the highly endangered plant communities of moist dune slacks (Grootjans et al. 2002). These measures include historical forms of land use, such as grazing, mowing and sod cutting, the latter of which appears to be the most promising tool for attaining habitats dominated by bare ground (Grootjans et al. 2001). It is likely that *T. ceperoi* would benefit from such conservation measures, particularly from the creation and stabilization of pioneer stages.

The common occurrence on the islands suggests that *T. ceperoi* is less threatened there than on the mainland, where it is restricted to anthropogenic habitats (Gröning et al. 2005). For *T. ceperoi* and many other pioneer species, it would be of crucial importance to restore dynamic riverine systems (Ingrisch et al. 1988). It has been shown that restored floodplains are quickly colonized by *T. ceperoi* (Gröning et al. 2005). Certainly, secondary habitats are also threatened by succession, since they are of anthropogenic origin and their sparse vegetation can only persist for a short pioneer phase. Active management of open habitats is, therefore, of crucial importance for the conservation of *T. ceperoi* and other hygrophilous pioneer species (Köhler 2001).

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