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ORIGINAL PAPER

Persisting in a windy habitat: population ecology and behavioral adaptations of two endemic grasshopper species in the Cape region (South Africa)

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Abstract Global biodiversity hotspots are rich in endemic insect species, many of which are threatened by the ongoing anthropogenic pressures on their habitats. The Cape region (South Africa) is one of these biodiversity hotspots, maintaining a high number of endemics. However, the ecology of most insect species in this region remains poorly understood. The two Orthoptera species *Betiscoides meridionalis* and *Betiscoides parva* are endemic to the Cape region and specialized on restio vegetation. They are threatened by increasing wildfire frequencies and invasions of non-native plant species. However, this information has been inferred from habitat changes, whereas no ecological study on these species has been conducted since they have been described. In order to facilitate conservation management, information on the ecology of these species is urgently required. The aim of our study was (1) to obtain data on the population ecology (particularly population sizes and mobility), and (2) to study the behavior of both species in response to environmental factors. For this purpose a mark-recapture-study and an observational behavior study were conducted. Both species had small population sizes and a low mobility with males moving greater distances than females. Wind had a strong influence on the behavior of *Betiscoides*, particularly on the small males of *B. parva*. Future studies might thus focus on the question whether wind-exposure is a critical factor for habitat choice of this species. We strongly recommend enhancing the connectivity of restio habitats and restoring these habitats to prevent extinction of specialized insect species.

Keywords Dispersal · Habitat connectivity · Habitat utilization · Orthoptera · Restionid fynbos · Wetland conservation

Introduction

The ongoing loss of biodiversity is a major concern of mankind and a large number of conservation organizations, projects and activities exist across the globe to tackle this problem. However, efficient conservation management is impossible without a sound knowledge of the ecology of threatened species (Gröning et al. 2007). Most conservation effort focuses on large charismatic vertebrates, particularly on large mammals and birds (Seddon et al. 2005). In contrast, the specific habitat requirements of threatened invertebrates are little understood (Cardoso et al. 2011). This data deficiency is illustrated by the high number of invertebrate species assessed as "Data Deficient" (DD) on the IUCN Red List of Threatened Species (28 % in version 2013.2), but also by the high number of outdated red list assessments, i.e. species that have not been re-assessed since >10 years (14.7 % in version 2013.2). However, even the existing red list assessments of invertebrate species are often based on insufficient information, particularly concerning population sizes and trends. Furthermore key information on habitat requirements and mobility of invertebrate species is often missing (Cardoso et al. 2011).

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Orthoptera are an important group of herbivorous insects, representing the most important primary consumers in many open-land ecosystems, such as savannahs, steppes and other grassland habitats (Odum et al. 1962). In Central Europe Orthoptera have become the most important insect group in conservation and landscape planning, due to their sensitivity to changes in land use intensity (Henle et al. 1999). However, very little is known about the ecology of tropical or subtropical Orthoptera species (Cowling et al. 1996), even though many of them may be threatened by extinction due to their small geographic ranges (Hochkirch 1998). The Cape region (South Africa) is one of the global hotspots of biodiversity, which is particularly rich in endemic plant and insect species (Linder 2003; Procheş and Cowling 2006). This is also true for Orthoptera, which occur in the Cape region with many flightless species (Naskrecki and Bazelet 2009). The grasshopper family Lentulidae consists of 98 grasshopper species (Eades et al. 2013), which are characterized by a small body size and the complete lack of wings and tympana (Dirsh 1965). The family has two major centers of endemism, one in the Cape region and a second one in the East African rainforests. One genus endemic to South Africa is the genus *Betiscoides*, which occurs with three species in the Cape region. The genus is strongly specialized on the plant family Restionaceae (Key 1937), where it is almost perfectly camouflaged due to its slender body shape. All three *Betiscoides* species have recently been assessed as “Endangered” on IUCN Red List of Threatened Species based on their small range sizes, their strong habitat fragmentation and the continuing decline in habitat caused by increasing wildfire frequencies, urbanization and invasions of non-native plant species (Hochkirch 2012). However, no specific research on their ecology or bionomics has been conducted since the species have been described by Sjöstedt (1923) and Key (1937). To promote conservation measures for these species, information on their habitat requirements, threats, population ecology and behavior is urgently required. In this study we focused on the two species *Betiscoides meridionalis* Sjöstedt, 1923 and *Betiscoides parva* Key, 1937. Our aim was to obtain knowledge on the mobility of these species and their behavior in response to environmental factors.

We focused on the following hypotheses: (1) the mobility of these species is low due to their flightlessness and their strong affiliation to restio vegetation; (2) the sexes of both species differ in behavioral patterns and mobility due to their sex-specific niche optima [with males being more active and more mobile as typical for Orthoptera, Hochkirch et al. (2007a)]; (3) the species and sexes differ in their behavioral response to abiotic factors (wind, temperature etc.) due to their differing body size.

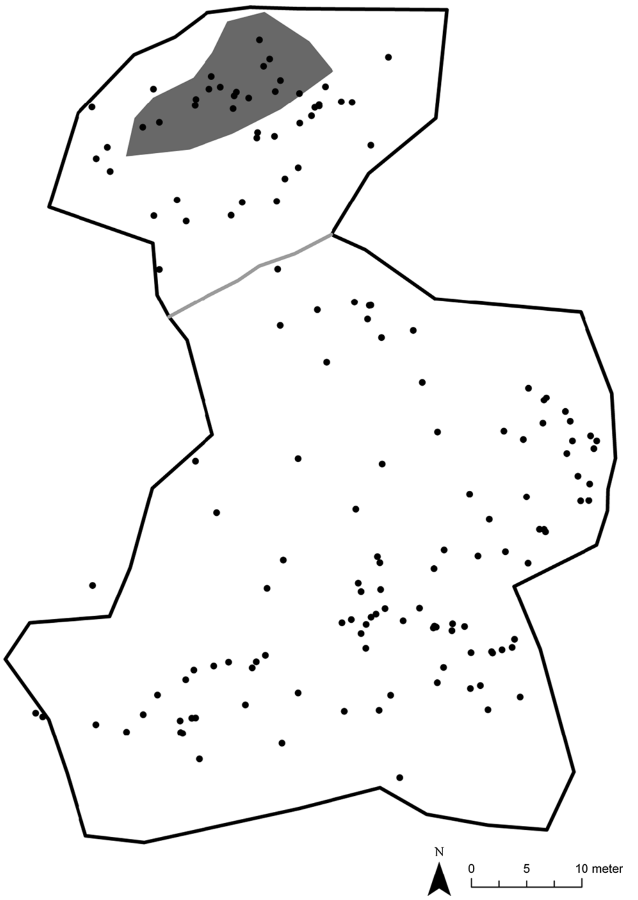

Fig. 1 Map of the Mark recapture site of *Betiscoides meridionalis* in Kogelberg Nature Reserve

Methods

Study species and study sites

Betiscoides species are strongly specialized on Restionaceae, a plant family belonging to the order Poales, being typical for the fynbos biome. They usually rest vertically on blades of Restionaceae, which they also use as food plant. *Betiscoides meridionalis* is the largest *Betiscoides* species (body length males: 37.5 mm, females: 42.5 mm, Key 1937), while *B. parva* represents the smallest *Betiscoides* species (body length males: 15 mm, females: 18.5 mm; Key 1937). *Betiscoides meridionalis* has a strongly elongated morphology with the vertex strongly projecting in front of the eyes and the antennal scape being situated close to the apex. *Betiscoides parva* has a much shorter and stouter body shape. The vertex projects only slightly in front of the eyes and the antennae are situated close to the eyes (Key 1937).

The study sites were situated in the Kogelberg Nature Reserve for *B. meridionalis* and in the Limietberg Nature Reserve for *B. parva*. Both reserves belong to the “Boland

Fig. 2 Map of the Mark recpature site of *Betiscoides parva* in Limietberg Nature Reserve

Area", which is part of the UNESCO World Heritage site "Cape Floral Region Protected Areas". The Kogelberg study sites were situated in the buffer zone of the reserve and had a calcareous, moist soil and maintained high stands of Restionaceae, which were surrounded by 1 year old Protaceae. The study site which was chosen for the behavioral study of *B. meridionalis* was situated on a slope (34°17′46.30″ S, 19°07′27.94″ E) whereas the study site for population size estimations was flat and covered an area of 3,199 m^2 (34°17′16.47″ S, 19°06′43.20″ E) (Fig. 1). The Limietberg study sites had a rather lime-deficient soil. The study site for population size estimations of *B. parva* was situated on a plateau (Fig. 2) and the soil lost moisture during the study period. This site was 1,841 m^2 (33°41′17.41″S, 19°05′41.94″E) and surrounded by 1 year old Proteaceae, which encroached successively into the site. Restionaceae were of medium size. The study site for behavioral study was flat and situated near a hiking trail (33°41′16.47″ S, 19°05′46.91″E). Due to a close stream the site showed constant soil moisture.

Data collection

The field data was collected in November and December 2012. A mark-recapture study was performed to estimate population sizes and obtain data on the mobility of both *Betiscoides* species. Each population was surveyed at least twice a week with a minimum gap of 24 h. We studied the population of *B. meridionalis* on 9 days between 20 November and 17 December 2012 and *B. parva* on ten days from 12 November to 14 December 2012. During each visit two observers walked in parallel curved lines across the complete study site and caught every detected individual by hand. Each adult individual was marked with a permanent non-toxic paint marker (Edding 780) using the 1-2-4-7 method (Buchweitz and Walter 1992). Due to the special morphology of *Betiscoides* we modified the marking method by placing the points laterally on the pronotum and the first abdominal tergites. The coordinates for each point of capture were measured with a differential GPS (Trimble GeoExplorer 2008 Series GeoXT; average precision 80–110 cm). The following parameters were recorded: species, sex, number of the individual, date, vegetation height, other remarks (e.g. specific characteristics of the individual). Afterwards, we released the individual at the catching position.

During the behavioral study, we observed a total of 81 individuals (*B. meridionalis*: 21 males and 21 female; *B. parva*: 20 males and 19 females) from 09 November to 14 December 2012. Each individual was observed for 30 min by two observers and its behavior was noted every 15 s. Afterwards, the individual was marked with a permanent marker (edding 780) to avoid pseudoreplication. After each observation, an individual of the opposite sex was chosen to minimize the influence of temporal effects. The following behaviors were distinguished (nomenclature following Uvarov 1977): resting, feeding, defecation, climbing up, climbing down, clambering (lateral movements through the vegetation), jumping, turning, antennal movements, leg movements, abdominal movements, abdominal undulations, peering (lateral head movements), cleaning with fore legs, cleaning with hind leg, resting, repeated touching (touching the vegetation with antenna). For data analysis, these were later summarized to the following categories: resting, feeding, defecation, locomotion (turning, clambering, jumping), climbing (climbing up, climbing down), repeated touching, movements (antennal, leg and abdominal movements and abdominal undulations, peering), cleaning (with for or hind legs). In addition we noted date, starting time, species, sex, observer, maximum vegetation height (in cm; measured with a folding rule), weather conditions, wind intensity close to the ground (estimated in three classes: windless (0), windless to breezy (1), breeze (2), medium to strong wind (3)), cloud cover (estimated in quarters), soil moisture (estimated in six classes from very dry (0) to wet (5)) and temperature (measured with an infrared thermometer; PeakTech 4990).

Statistical analyses

The population sizes were estimated in MARK 6.2 (White and Burnham 1999) using the module POPAN, which performs Jolly-Seber calculations and is suitable for open populations with varying death and recruitment rates over time. POPAN 5.0 uses a Maximum Likelihood approach to estimate three parameters based on mark-recapture data: Phi is the daily residence rate as the number of individuals at the site combining mortality and emigration, p_i is the daily catch ability and $pent_i$ the daily recruitment combining the percentage of "birth" (in this case final moult) and immigration. Based on these first three parameters, B_i (the daily recruitment), N_i (the daily population size) and N (the total population size) are derived (Fric et al. 2010). We first calculated the full model (Phi(g*t)p(g*t)pent(g*t)N(g); with g = sex, t = time) and performed a goodness of fit test using the Tests 2 and 3 of the RELEASE suite in MARK to check the data quality. These test violations against the assumptions that (1) every marked animal, which is present in a population at a given time has the same recapture probability (p_i) and (2) that every marked animal has the same survival probability to the next time step. Afterwards we calculated the predefined models and simplified them in order to reduce the number of utilized parameters. For each response variable (Phi, p, pent, N), we first used the interaction term between sex and time (g*t) as explanatory variable. Subsequently we used the addition of sex and time (g + t) and then tested sex (g) and time (t) independently as well as each of the parameters as "constant" (.). Each possible combination of these factors was calculated and the Akaike information criterion (AIC) was used to find the best fitting model.

Geographical distances were calculated with ArcView GIS 3.2 (ESRI) using the extensions ''Animal Movement'' and ''Home Range Analysis''. The calculation of distances was based on all individuals that were captured at least twice (*B. meridionalis* n = 48; *B. parva* n = 64). The linear distance between two consecutive captures of each individual was measured. Based on these data we calculated the single movement distances for each individual with the function "Calculate Interfix Distance", which were later standardized by the number of days between the catches. The addition of all single distances revealed the cumulative movement distance for each individual. The maximum distance (i.e. the largest distance between all recorded positions of an individual) between three or more observations of an individual was also calculated using "Calculate Distance". Cumulative distance and maximum distance were tested in a two way ANOVA to detect possible differences between the species and sexes. For this purpose the data were Box-Cox-transformed using Venables and Ripley's MASS library for R (Venables and Ripley 2002) to derive the optimal exponent (λ) for fitting the data to the models assumptions.

For analyzing the behavioral data, we first calculated the relative frequencies of each behavior type for each specimen. This was done to correct for incomplete observations caused by the disappearance of some individuals during the observation time (n = 14). We performed multifactorial covariance analyses (ANCOVA) to test for the effects of species and sex and the effects of wind intensity, weather condition, cloud cover, maximum vegetation height, temperature, soil moisture and time (explanatory variables) on the frequency of each behavior type (response variable). Again we performed Box-Cox transformations to assure an optimal fit of the data to the model assumptions. Each model was simplified using the "step" function in R. A Principal Component Analysis (PCA) was performed in the "vegan" 2.0-8 package for R (Oksanen et al. 2008) to simplify the behavioral data. The correlations of the species, sexes and the covariates with the frequency of each behavior type were tested for significance with the function "env.fit" (environmental fitting) using 1,000 permutations.

Table 1 Estimated population size for *Betiscoides meridionalis* (model {Phi(g + T) p(g) pent(t) N(g)}) and *Betiscoides parva* (model {Phi(.) p(t) pent(t) N(.)})

Betiscoides meridionalis					*Betiscoides parva*				
	N*	SE ±	Min	Max		N*	SE ±	Min	Max
♂	92	18	56	127	♂	338	67	207	469
♀	119	23	74	164	♀	335	67	204	466

N*: total population size, *SE* standard error, *Min* minimum population size, *Max* maximum population size

Results

Population sizes

In total we caught 103 individuals of *B. meridionalis*, 48 of which were recaptured and 213 individuals of *B. parva* (64 recaptured). Thus, the recapture rate was 46.6 % for *B. meridionalis* and 30 % for *B. parva* with no significant differences between the sexes for both species ($\chi^2 = 0.4154$, $df = 1$, $p = 0.5193$). For *B. meridionalis,* the best fitting model for the population size was {Phi(g + T) p(g) pent(t) N(g)}, suggesting a strong difference between the sexes in residence rate, catchability and population size, a linear correlation between survival rate and time, and a non-linear effect of time on recruitment. For *B. parva* the best fitting model was {Phi(.) p(t) pent(t) N(.)}, which means that there was a temporal effect on capture probability and recruitment, while survival and population size were independent of sex or time. The two next best fitting models performed only slightly worse (Tab. S1) and estimated population sizes hardly differed (Table 1).

The best population size estimate for *B. meridionalis* was 211 individuals consisting of 119 females (±23 SE) and 92 males (±18 SE). For *B. parva* the estimated population size was 673 (338 males ± 67 SE and 335

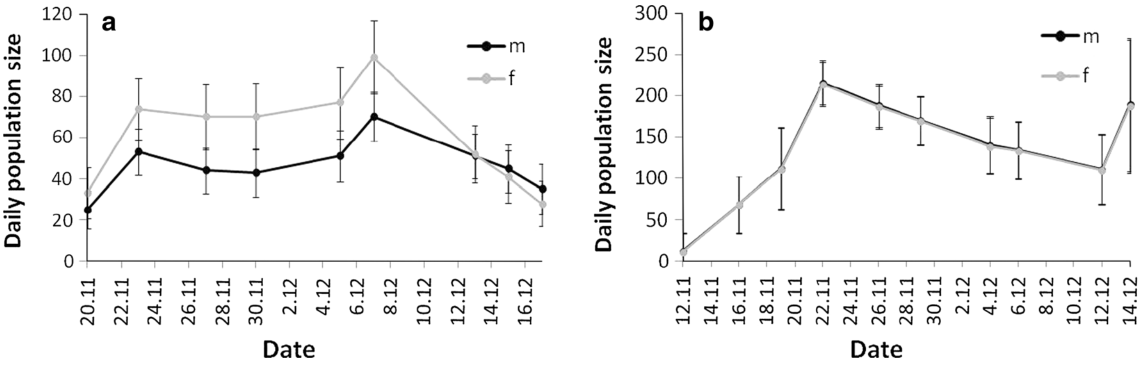

Fig. 3 Estimated daily population sizes for *B. meridionalis* (**a**; model {Phi(g + T) p(g) pent(t) N(g)}) and *B. parva* (**b**; model {Phi(.) p(t) pent(t) N(.)})

Table 2 Mean daily distance, maximum distance and cumulative distance for *B. meridionalis* and *B. parva* (standard errors in parentheses)

	Daily distance ø	Maximum distance ø	Cumulative distance ø
B. meridionalis			
♂	2.5 (0.7)	15.1 (4.6)	14.7 (4.2)
♀	0.5 (0.1)	6.1 (1.0)	4.9 (1.1)
B. parva			
♂	1.1 (0.1)	13.3 (4.3)	12.1 (1.8)
♀	0.7 (0.2)	11.5 (3.8)	6.3 (1.3)

females ± 67 SE). These population sizes could be translated into a population density of 0.1 individuals per m^2 for *B. meridionalis* and 0.4 individuals per m^2 for *B. parva*. The daily population sizes increased for both species during our study period and decreased later again (Fig. 3). However, in *B. parva* the maximum population size occurred approximately 2 weeks earlier (22 Nov) than in *B. meridionalis* (07 Dec; Fig. 1).

Mobility

The sexes differed significantly in their mobility. Males were generally more mobile than females, regarding the cumulative distance (ANOVA, $\lambda = 0.01$, $F_{1,83} = 17.9$, $p \leq 0.001$) as well as the maximum distance (ANOVA, $\lambda = 0.08$, $F_{1,83} = 18.2$, $p \leq 0.001$), whereas the daily distance did not differ significantly (Table 2). No significant difference was detected between the species (cumulative distance: ANOVA, $\lambda = 0.01$, $F_{1,83} = 0.7639$, $p \leq 0.3846$; maximum distance: ANOVA, $\lambda = 0.08$, $F_{1,83} = 1.0305$, $p \leq 0.3130$). Approximately 60 % of the females of both species migrated less than 0.5 m per day, males of both species crossed cumulative distances up to 15 m.

Behavior

In both species and sexes the most frequent behavior was resting (c. 60 % of all observations). Interspecific and intersexual differences were detected for cleaning, climbing and defecation. Particularly, males of *B. parva* spent significantly more time on cleaning and less time on climbing. *B. parva* defecated significantly more often than *B. meridionalis* and males more often than females. A significant interaction between sex and vegetation height was found for feeding. Feeding activity of males decreased with increasing vegetation height (Table 3).

Among environmental factors, wind had the strongest influence on the behavior of *Betiscoides*. Climbing and locomotion generally decreased with increasing wind strength, but we found strong differences between species and sexes. Males of *B. parva* showed a strong response of climbing activity to wind strength, whereas in *B. meridionalis* no effect of wind was found (Fig. 4). For the most common behavior type (resting), we found a significant interaction between species, sex and wind. *B. parva* males were more often found resting at higher wind strengths, whereas *B. meridionalis* and *B. parva* females did not show such a strong response to wind. Furthermore, we found significant effects of vegetation height and temperature on the behavior of *Betiscoides*. Males showed less locomotion and feeding activity with increasing vegetation height. Higher temperatures resulted in increased locomotion but decreased the frequency of repeated touching.

The first two principal components explained 49.4 % of the behavioral variance with the first function being explained mainly by resting (score: −1.68) and climbing (score: 1.30) and the second function being explained by feeding (score: 1.34) and defecation (score: 1.01). Environmental fitting showed a significant correlation of *B. parva* with the PCA (Environmental Fitting, $p \leq 0.001$) as well as a significant correlation of wind strength with the

Table 3 Significant factors and interactions in the simplified models of multifactorial covariance analyses (ANCOVA) using the explanatory variables species, sex, weather, temperature and wind and behavior as the response variable

Behavior	Factor	λ	*P* value	F value
Locomotion	Species:sex:weather	0.37	0.002	$F_{1.73} = 9.841$
Climbing	Species	0.38	0.03	$F_{1.73} = 4.695$
	Wind	0.38	0.04	$F_{1.73} = 4.392$
	Species:wind	0.38	0.03	$F_{1.73} = 4.835$
	Species:sex	0.38	0.04	$F_{1.73} = 4.531$
	Species:sex:wind	0.38	0.01	$F_{1.73} = 7.524$
Movement	Wind	0.37	0.04	$F_{1.76} = 4.425$
	Vegetation height	0.36	0.03	$F_{1.73} = 5.124$
	Species:sex	0.39	0.03	$F_{1.73} = 4.661$
	Species:sex:temperature	0.39	0.04	$F_{1.73} = 4.467$
Cleaning	Species	−0.06	0.02	$F_{1.73} = 5.467$
	Wind	−0.06	0.03	$F_{1.73} = 4.732$
	Species:sex	−0.06	0.04	$F_{1.73} = 4.210$
	Species:sex:wind	−0.06	0.03	$F_{1.73} = 5.174$
Feeding	Sex:vegetation height	−0.05	0.03	$F_{1.75} = 5.067$
Defecation	Species	−0.15	≤ 0.001	$F_{1.76} = 18.594$
	Sex	−0.15	0.02	$F_{1.76} = 5.231$
Resting	Species:sex:wind	1.6	0.05	$F_{1.73} = 3.868$
Repeated	Day	0.2	≤ 0.001	$F_{1.73} = 12.341$
Touching	Temperature	0.2	0.04	$F_{1.75} = 4.190$
	Sex:temperature	0.2	0.01	$F_{1.75} = 6.570$

Only significant factors and interactions are shown (p value ≤ 0.05)

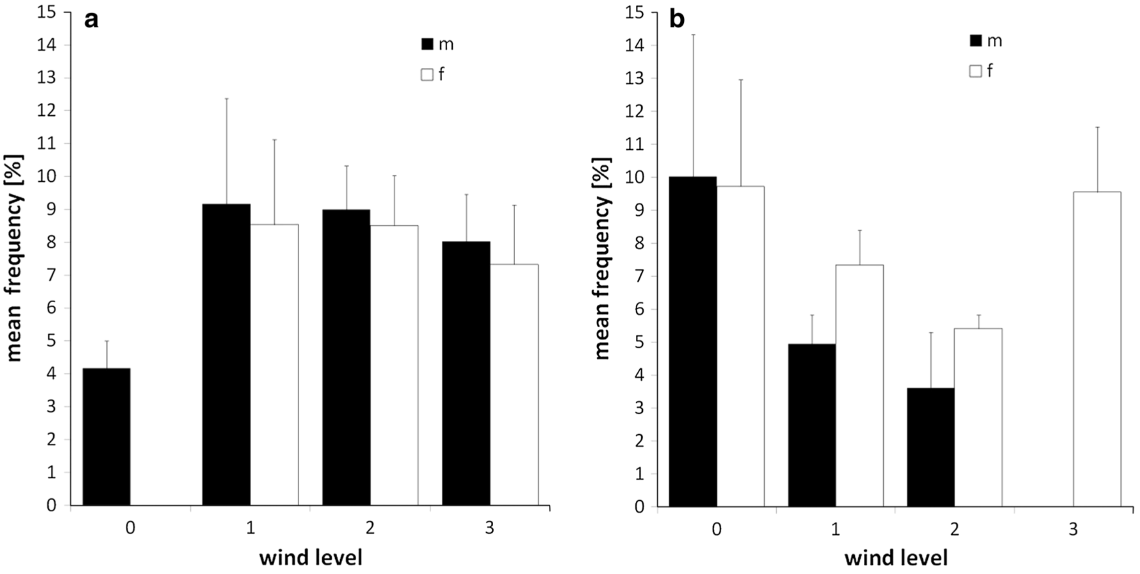

Fig. 4 Mean frequency of the behavior “climbing” at different wind levels for *Betiscoides meridionalis* (**a**) and *Betiscoides parva* (**b**); *error bars* are standard errors

PCA (Environmental Fitting, $p = 0.02$). Vegetation height showed only a slight trend ($p = 0.1$) for a correlation.

The strong positive correlation of *B. parva* males with the second PCA function was mainly associated with lower activity compared to *B. parva* females and *B. meridionalis* specimens. The strong influence of wind strength on the behavior of *B. parva* males also led to a negative correlation between wind strength and the second PCA function (Fig. 5).

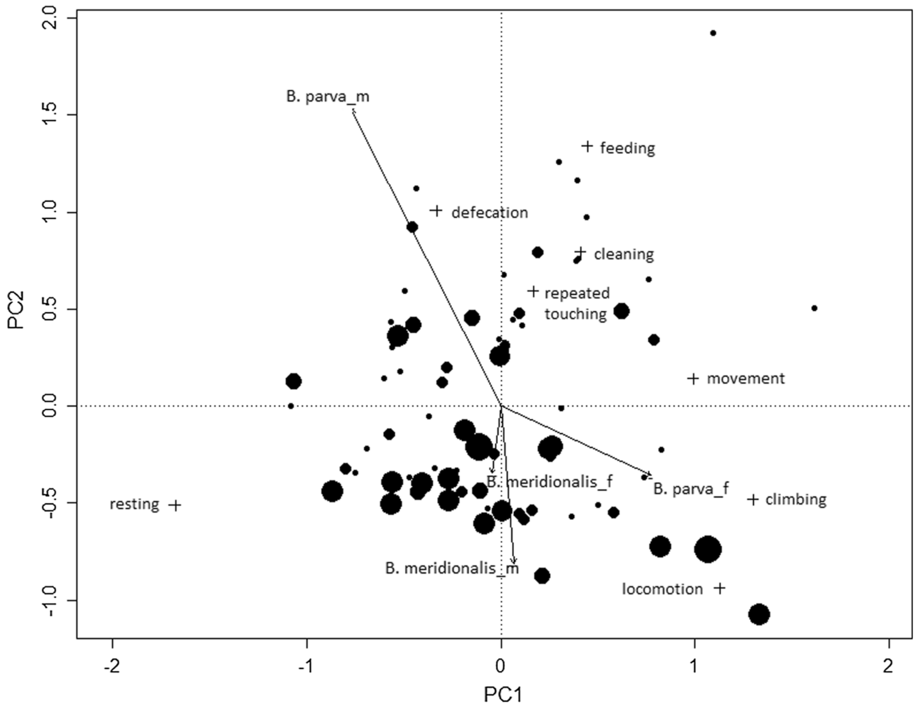

Fig. 5 Plot of the first two axes of the principal component analysis on the behavior of *Betiscoides meridionalis* and *B. parva*. Each circle represents one individual with its size normalized by wind level

Discussion

The influence of wind on behavior

Many Orthoptera species show behavioral adaptations to their habitat (Sänger 1977). *Betiscoides* species are strongly affiliated with restio vegetation. Their elongated morphology together with their cryptic (often striped) coloration provides an ideal camouflage. They rest and move mainly in a vertical position and often show "clambering"—a vertical climbing movement through the vegetation, which is typical for graminicolous grasshopper species (Uvarov 1977). Furthermore, they have the typical dodging behavior (hiding behind the blade when disturbed), which is also known from other Orthoptera species associated with high vertical vegetation structure (Uvarov 1977). Our results show that wind has a strong influence on the behavior of *Betiscoides*, particularly on males of *B. parva*. Several activities (climbing, cleaning and movements) decreased with increasing wind intensity. One possible reason for this might be convective heat loss (as the convective heat transfer coefficient changes with wind speed and insect size), which increases with higher wind speed (Lactin and Johnson 1998). Physiology and activity of poikilothermic animals, like grasshoppers, are affected by heat loss. It is generally known that Orthoptera species become less active during high wind speed (Nielsen and Dreisig 1970; Stiedl and Bickmeyer 1991). However, there might also be a direct influence of wind on the behavior of these small insects, or an influence of the moving vegetation. *Betiscoides* are usually found in a vertical position on restio blades, where they are exposed to stronger winds than, for example, terricolous Orthoptera species. Both hypotheses (convective heat loss and direct physical effects) would explain why *B. parva* males (which are the smallest among the insects studied) show the strongest response to wind, although wind levels were much lower in the habitat of this species than in the habitat of *B. meridionalis* (Fig. 2).

It is well known that macro-, meso- and microclimate have a strong influence on the habitat preferences of Orthoptera (Weiss et al. 2013). Adaptation of the egg pods and egg morphology to different levels of soil moisture is known to be critical for the habitat affiliation of many species (Ingrisch 1983). We observed that both *Betiscoides* species oviposit into the ground. The strong association with moist habitats might thus be a result of the water requirements of the eggs (Ingrisch 1983), but it might also be an indirect effect of its specialization on Restionaceae as host plant. Moreover, the temperature sums received during nymphal development often determine the association of Orthoptera with climatically favorable habitats and the location of their range margins (Ingrisch and Köhler 1998). In contrast to soil moisture and temperature, the effect of wind exposure on habitat affiliation of grasshoppers is little understood (Gardiner and Dover 2008). Lewis (1969) found out that small, flightless insects gather near fences to assure optimal wind protection. Furthermore, wind protection seems to influence the distribution of Orthoptera on agricultural areas in temperate areas (Gardiner and Dover 2008). Our results suggest that even in climatically favorable regions, wind may strongly affect the behavior of small graminicolous grasshopper species. The significance of wind exposure as determinant of the presence or absence of these species from restio sites (particularly *B. parva*) requires further investigation. So far it remains unknown, whether males of *B. parva* simply show a stronger reaction to wind or whether these effects are also critical to its survival.

Phenology and population sizes

Little is known about the phenology of most tropical and subtropical grasshopper species. For *B. meridionalis* it had been stated that adults can be found from January onwards (Picker et al. 2004). Our results show that a first complete generation of adults occurs already in early spring (late October). The course of daily population sizes indicates that our observations covered a complete adult spring generation. The first nymphs of the next generation of *B. parva* were found on 6 December, illustrating a slight overlap of the generations. We also found adult *Betiscoides* (as well as nymphs) during visits in late summer throughout the Cape region, suggesting that more than these two generations occur per year. The mild climate in the Cape Region might promote such multivoltine life cycles. As the developmental speed and hatching date of Orthoptera is strongly affected by climate (Hewitt 1979), the delayed phenology of *B. meridionalis* compared to *B. parva* might be a result of the differing climate of the sites. Kogelberg is located closer to the Atlantic Ocean than Limietberg and, therefore, has a more maritime climate.

As typical for the Cape region, the estimated population sizes of both species were rather small (Kemper et al. 1999). However, it needs to be considered that only single populations of the two *Betiscoides* species have been studied. Larger populations might occur in larger habitats. However, encroachment of invasive plants and increasing wildfire frequencies threaten these ecosystems and might thus have negative effects on the population trends of *Betiscoides*. Highly specialized Orthoptera species are often confined to small areas of suitable habitat and might thus only reach small population sizes (Hochkirch et al. 2008). On the other hand, population sizes of Orthoptera are often underestimated (Weyer et al. 2012; Gardiner et al. 2005; Larson et al. 1999) and other wetland specialists, such as *Chorthippus montanus*, have been shown to reach population sizes of up to 1,000 individuals (Weyer et al. 2012). Due to their strong adaptation to Restionaceae it is likely that the population sizes of *Betiscoides* correlate with the size of their habitat.

Mobility

Both *Betiscoides* species are completely flightless and showed a very low mobility. Average daily distances, cumulative distances as well as maximum distances were even lower than in other flightless grasshoppers (Diekötter et al. 2005; Kindvall 1999), whereas winged grasshopper species are generally much more mobile (Hein et al. 2003; Buchweitz and Walter 1992; Maes et al. 2006). This extraordinary low mobility might also be explained by the strong adaptation to Restionaceae. The main types of locomotion in *Betiscoides* are climbing and clambering. Even when disturbed, the species prefers to dodge around a blade over jumping. Escape jumps are usually short and the individuals immediately climb down the next blade. As the restio vegetation provides all necessary resources to fulfill the complete the life cycle of *Betiscoides*, there is probably no strong selective pressure on mobility of these grasshoppers. Intersexual differences in mobility are quite common among grasshoppers (Ingrisch and Köhler 1998). Males are usually more mobile as they spend more time for mate finding (Hochkirch et al. 2007a). The higher mobility of *B. meridionalis* males compared to *B. parva* might be caused by its lower population density and a stronger need for locomotion to find mates. Other factors which are known to influence mobility of Orthoptera are habitat fragmentation and habitat degradation (Kindvall 1999; Berggren 2004; Gardiner and Hill 2004). Many insect species show higher mobility in less suitable habitat. In fact, the habitat of *B. meridionalis* was small and influenced by pollution, which might also have caused the higher mobility.

Conservation of *Betiscoides*

Small flightless Orthoptera species are known to be at higher risk of extinction than winged species due to their small dispersal capability (Reinhardt et al. 2005; Witzenberger and Hochkirch 2008). As all Lentulidae are flightless, it is likely that other species of this family are threatened as well. However, the ecology of most Lentulidae remains unknown and even the taxonomy is probably far from complete. A recent revision of the flightless grasshopper genus *Euloryma* has uncovered the existence of >20 cryptic species in the Cape region (Spearman 2013) and first molecular data suggests that something similar is true for *Betiscoides* (Matenaar unpubl.). Our study represents the first ecological study of Cape-endemic lentulid species. It is very likely that other lentulid species have a similar ecology, particularly concerning their low mobility and strong habitat affiliation. It will be important to obtain more data on their habitats, distribution, population sizes and trends to facilitate their conservation.

Although both *Betiscoides* species occur in nature reserves belonging to the UNESCO world heritage site "Cape Floral Region Protected Areas", they are still under threat due to the increasing wildfire frequencies and invasions of non-native species, which are difficult to manage even in protected areas (Richardson and van Wilgen 2004). The population of *B. meridionalis* has been studied in the buffer zone of Kogelberg Nature Reserve. The small size of this population indicates that it might be insufficiently robust against environmental fluctuations and it might thus have a higher extinction probability. This could be the result of an insufficient management in the buffer zone as we found scrap and screws on the site and oil pollution in a stream nearby. Grant and Samways (2011) already reported that degenerated buffer zones of reserves may often support more generalized species but do not necessarily conserve endemic or threatened species. The habitat in the studied area is rather fragmented making recolonization unlikely and increasing extinction risk (Hochkirch et al. 2007b). The maintenance of large restio stands in the moist areas of the Cape fynbos is consequently of high importance for the protection of these species. As the mobility of both species is very limited, the colonization or recolonization probability of new or recovering restio stands is very low. In many cases it may be too slow to keep up with habitat destructions caused by fire or invasive plant species. Furthermore, our study shows that not all restio stands are suitable for all *Betiscoides* species, as *B. parva* seems not to be able to colonize areas which are prone to heavy winds. Although wind might be less problematic for *B. meridionalis*, it remains unclear whether other factors exist that limit its distribution in addition to the occurrence of Restionaceae.

Increasing wildfire frequencies are threatening large parts of the endemic Cape flora and fauna. Both Kogelberg and Limietberg Nature Reserves have been severely affected by fire during the last three years. Limietberg even lost 80 % of its vegetation due to fire during this period (Swarts pers. comm.) and consequently the vegetation was still young during our study. Wildfires are a natural source of disturbance in the fynbos ecosystem and it is known that many Orthoptera species are little sensitive or even positively affected by fire (Hochkirch and Adorf 2007). However, the anthropogenic increase in fire frequency has already caused a decrease in floral diversity during the last years, because the plants are not able to produce enough seeds on time (Hugo pers. comm.). The lack of habitat connectivity (particularly in areas between the reserves) together with the increased wildfire cycles is a major threat to *Betiscoides* species and probably also other arthropods associated with the restio vegetation. Hence, these conditions might cause the extinction of the observed population of *B. meridionalis*, if no appropriate management for the buffer zones is established on time. Although we detected further 22 populations of *B. meridionalis* and 25 populations of *B. parva* on 46 study sites in nature reserves of the Cape region, the sizes of these populations remain unknown and the threats to them poorly understood. As *Betiscoides* species are completely flightless, they are likely to be affected by habitat fragmentation and the loss of each population would decrease this connectivity. In order to improve the conservation of restio specialists, it is important to instigate habitat restoration measures in areas where such vegetation has been lost and to preserve small patches of restio vegetation which are currently outside the reserves. This might help to improve the connectivity of the remaining populations of such species. Furthermore, strategic plans for the control of wildfires and invasive plant species, like *Ornithogalum thyrsoides* (Kempler et al. 1999), are necessary. Finally, it is particularly important to map the occurrence of endemic insects in the Cape region in order to identify key areas for insect conservation and prevent these from sudden extinction caused by carelessness.

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References

Berggren Å (2004) Impact of grazing on individual male movement in Roesel’s Bush-Cricket *Metrioptera roeseli*: one possible clue to species range expansion. J Insect Behav 17:419–429. doi:10.1023/B:JOIR.0000042531.27859.ac

Buchweitz M, Walter R (1992) Individualmarkierung von Heuschrecken - ein Erfahrungsbericht. Articulata 7:55–61

Cardoso P, Erwin TL, Borges PA et al (2011) The seven impediments in invertebrate conservation and how to overcome them. Biodivers Conserv 144:2647–2655. doi:10.1016/j.biocon.2011.07.024

Cowling RM, Macdonald I, Simmons M (1996) The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. Biodivers Conserv 5:527–555

Diekötter T, Csencsics D, Rothenbuhler C et al (2005) Movement and dispersal patterns in the bush cricket *Pholidoptera griseoaptera*: the role of developmental stage and sex. Ecol Entomol 30:419–427. doi:10.1111/j.0307-6946.2005.00714.x

Dirsh VM (1965) The African genera of Acridoidea. Cambridge University Press, Cambridge

Eades D, Otte D, Cigliano M.M et al (2013) Orthoptera Species File. Version 5.0/5.0. orthoptera.speciesfile.org. Accessed 17 Oct 2013

Fric Z, Hula V, Klimova M et al (2010) Dispersal of four fritillary butterflies within identical landscape. Ecol Res 25:543–552. doi:10.1007/s11284-009-0684-4

Gardiner T, Dover J (2008) Is microclimate important for Orthoptera in open landscapes? J Insect Conserv 12:705–709. doi:10.1007/s10841-007-9104-7

Gardiner T, Hill J (2004) Directional dispersal patterns of *Chorthippus parallelus* (Orthoptera: Acrididae) in patches of grazed pastures. J Orthopt Res 13:135–141

Gardiner T, Hill J, Chesmore D (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in Grassland ecosystems. J Insect Conserv 9:151–173. doi:10.1007/s10841-005-2854-1

Grant PB, Samways MJ (2011) Micro-hotspot determination and buffer zone value for Odonata in a globally significant biosphere reserve. Biol Conserv 144:772–781. doi:10.1016/j.biocon.2010.11.008

Gröning J, Krause S, Hochkirch A (2007) Habitat preferences of an endangered insect species, Cepero's ground-hopper (*Tetrix ceperoi*). Ecol Res 22:767–773. doi:10.1007/s11284-006-0315-2

Hein S, Gombert J, Hovestadt T et al (2003) Movement patterns of the bush cricket *Platycleis albopunctata* in different types of habitat: matrix is not always matrix. Ecol Entomol 28:432–438. doi:10.1046/j.1365-2311.2003.00531.x

Henle K, Amler K, Biedermann R, Kaule G, Poschlod B (1999) Bedeutung und Funktion von Arten und Lebensgemeinschaften in der Planung. In: Amler K, Bahl A, Henle K et al (eds) Populationsbiologie in der Naturschutzpraxis. Ulmer, Stuttgart, pp 17–23

Hewitt GB (1979) Hatching and development of rangeland grasshoppers in relation to forage growth, temperature, and precipitation. Environ Entomol 8:24–29

Hochkirch A (1998) A comparison of the grasshopper fauna (Orthoptera: Acridoidea & Eumastacoidea) of the Uluguru Mountains and the East Usambara Mountains, Tanzania. J E Afr Nat Hist 87:221–232

Hochkirch A (2012) *Betiscoides meridionalis*. www.iucnredlist.org. Accessed 13 Oct 2013

Hochkirch A, Adorf F (2007) Effects of prescribed burning and wildfires on Orthoptera in Central European peat bogs. Environ Conserv 34:225–235. doi:10.1017/S0376892907004006

Hochkirch A, Gröning J, Krause S (2007a) Intersexual niche segregation in Cepero's Ground-hopper, *Tetrix ceperoi*. Evol Ecol 21:727–738. doi:10.1007/s10682-006-9147-3

Hochkirch A, Witzenberger KA, Teerling A, Niemeyer F (2007b) Translocation of an endangered insect species, the field cricket (*Gryllus campestris* Linnaeus, 1758) in northern Germany. Biodivers Conserv 16:3597–3607. doi:10.1007/s10531-006-9123-9

Hochkirch A, Gärtner A, Brandt T (2008) Effects of forest-dune ecotone management on the endangered heath grasshopper, *Chorthippus vagans* (Orthoptera: Acrididae). Bull Entomol Res 98:449–456. doi:10.1017/S0007485308005762

Ingrisch S, Köhler G (1998) Die Heuschrecken Mitteleuropas. Westarp Wissenschaften, Magdeburg

Kemper J, Cowling RM, Richardson DM (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. Biodivers Conserv 90:103–111

Key K (1937) New Acridiidae from South Africa. Ann S Afr Mus 32:135–167

Kindvall O (1999) Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tettigoniidae). J Anim Ecology 68:172–185. doi:10.1046/j.1365-2656.1999.00273.x

Lactin DJ, Johnson DL (1998) Environmental, physical and behavioral determinanta of body temperature in grasshopper Nymphs (Orthoptera: Acrididae). Can Entomol 130:551–577. doi:10.4039/Ent130551-5

Larson DP, O'Neill KM, Kemp WP (1999) Evaluation of the accuracy of sweep sampling in determining grasshopper (Orthoptera: Acrididae) community composition. J Agric Urban Entomol 16:207–214

Lewis T (1969) The diversity of the insect fauna in a hedgerow and neighbouring fields. J Appl Ecol 6:453–458

Linder HP (2003) The radiation of the Cape flora, southern Africa. Biol Rev Camb Philos Soc 78:597–638

Maes D, Ghesquiere A, Logie M et al (2006) Habitat use and mobility of two threatened coastal dune insects: implications for conservation. J Insect Conserv 10:105–115. doi:10.1007/s10841-006-6287-2

Naskrecki P, Bazelet CS (2009) A species radiation among South African flightless spring katydids (Orthoptera: Tettigoniidae: Phaneropterinae: Brinckiella Chopard). Zootaxa 2056:46–62

Nielsen ET, Dreisig H (1970) The Behavior of Stridulation in Orthoptera Ensifera. Behavior 37:205–252

Odum EP, Connell CE, Davenport LB (1962) Population energy flow of three primary consumer components of old-field ecosystems. Ecology 43:88–96

Oksanen J, Kindt R, Legendre P et al (2008) The vegan package. Community ecology package. http://vegan.r-forge.r-project.org/. Accessed 13 Oct 2013

Picker M, Griffiths CL, Weaving A (2004) Field guide to insects of South Africa. Struik, Cape Town

Procheş Ş, Cowling RM (2006) Insect diversity in Cape fynbos and neighbouring South African vegetation. Global Ecol Biogeogr 15:445–451. doi:10.1111/j.1466-822X.2006.00239.x

Reinhardt K, Köhler G, Maas S et al (2005) Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. Ecography 28:593–602. doi:10.1111/j.2005.0906-7590.04285.x

Richardson DM, van Wilgen BW (2004) Invasive alien plants in South Africa: How well do we understand the ecological impacts? S Afr J Sci 100:45–52

Sänger K (1977) Über die Beziehungen zwischen Heuschrecken und der Raumstruktur ihrer Habitate. Zool Jb Syst 104:433–488

Seddon PJ, Soorae PS, Launay F (2005) Taxonomic bias in reintroduction projects. Anim Conserv 8:51–58. doi:10.1017/S1367943004001799

Spearman L (2013) Taxonomic revision of the South African Grasshopper Genus *Euloryma* (Orthoptera: Acrididae). Trans Am Entomol Soc 139:1–111

Stiedl O, Bickmeyer U (1991) Acoustic behaviour of *Ephippiger ephippiger fiebig* (Orthoptera, Tettigoniidae) within a habitat of Southern France. Behav Process 23:125–135. doi:10.1016/0376-6357(91)90063-6

Uvarov B (1977) Grasshoppers and Locusts—a handbook of general Acridology, vol 2. Cambridge University Press, Cambridge

Venables WN, Ripley BN (2002) Modern applied statistics with S-Plus. Springer, New York

Weiss N, Zucchi H, Hochkirch A (2013) The effects of grassland management and aspect on Orthoptera diversity and abundance: site conditions are as important as management. Biodivers Conserv 22:2167–2178. doi:10.1007/s10531-012-0398-8

Weyer J, Weinberger J, Hochkirch A (2012) Mobility and microhabitat utilization in a flightless wetland grasshopper, *Chorthippus montanus* (Charpentier, 1825). J Insect Conserv 16:379–390. doi:10.1007/s10841-011-9423-6

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139. doi:10.1080/00063659909477239

Witzenberger KA, Hochkirch A (2008) Genetic consequences of animal translocations: a case study using the field cricket, *Gryllus campestris L.* Biol Conserv 141:3059–3068. doi:10.1016/j.biocon.2008.09.017