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Conservation management of coastal dunes for Orthoptera has to consider oviposition and nymphal preferences

Yvonne Wünsch · Jens Schirmel · Thomas Fartmann

Abstract Dune and heathland ecosystems can harbour a multitude of specialized insect species. To assess the habitat quality of these ecosystems, the presence of specialized insect species may act as a useful indicator. The Orthoptera species *Myrmeleotettix maculatus*, *Decticus verrucivorus*, and *Platycleis albopunctata* present such umbrella species. Because knowledge of oviposition and nymphal habitats of these species is insufficient, we conducted a combined study consisting of an outdoor oviposition experiment and a field survey analyzing nymphal habitat preferences during summer 2009 on the Baltic island of Hiddensee, Germany. The oviposition experiment showed, that all three species mostly avoid oviposition under lichens (= mature grey dunes). *M. maculatus* preferred bare ground for oviposition, *D. verrucivorus* favoured both bare ground and mosses, and *P. albopunctata* laid most eggs into mosses. Young nymphs of both *M. maculatus* and *P. albopunctata* preferred initial grey dunes with a high proportion of bare ground and moss-rich grey dunes. Old nymphs were related to moss-rich and lichen-rich grey dunes with more dense vegetation. Based on our results, early seral stages of dune succession with bare ground and mosses as keystone structures are crucial for the conservation of the three studied umbrella species. Because old nymphs and adults additionally require more dense grey dune vegetation or adjacent heath stands, practical dune and heathland management measures should aim to maintain a mosaic-like pattern of different grey dune and dwarf-shrub vegetation stands.

Keywords Caelifera · Ensifera · Grasshopper · Habitat requirement · Heathland

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Introduction

Dune and heathland ecosystems can harbour high numbers of insects with a multitude of specialized species (Maes and Bonte 2006; Maes et al. 2006; Schirmel et al. 2010a). Nowadays these habitats are threatened and therefore protected by the EU Habitats Directive (Ssymank et al. 1998). The main threats are loss of natural sand dynamics, enhanced nitrogen deposition, and the abandonment of land use (grazing), resulting in eutrophication of these nutrient-poor ecosystems including grass and shrub encroachment (Webb 1998; Ketner-Oostra and Sykora 2004; Maes and Bonte 2006; Remke et al. 2009).

To assess habitat quality of dunes and heathlands, the presence of specialized and typical insect species may act as a useful indicator (Maes and Bonte 2006). Orthoptera (Ensifera and Caelifera) contain such umbrella species. In general, Orthoptera are a suitable insect group for monitoring terrestrial ecosystems (Poniatowski and Fartmann

2008). They take an important position in food webs and are sensitive to environmental changes such as grazing and abandonment (Curry 1994; Báldi and Kisbenedek 1997; Fartmann and Mattes 1997; Schirmel et al. 2010a). In addition, several specialized, xerothermic Orthoptera species occur in dune and heathland ecosystems (Wranik et al. 2008; Schirmel et al. 2010a). In Central and North-Western Europe typical species in such habitats are the Caelifera *Myrmeleotettix maculatus* (Thunberg 1815) and the Ensifera *Decticus verrucivorus* (Linnaeus 1758) and *Platycleis albopunctata* (Goeze 1778) (Haes and Harding 1997; Kleukers et al. 1997; Detzel 1998; Maas et al. 2003; Schirmel et al. 2010a, b). Especially *D. verrucivorus* and *P. albopunctata* are endangered in many regions (e.g. Great Britain: Haes and Harding 1997; Netherlands: Kleukers 2001; Northern Germany: Maas et al. 2002) and target species of special conservation interest (e.g. Cherrill and Brown 1990b; Hjermann and Ims 1996; Hein et al. 2007).

In order to preserve such target species, knowledge about habitat requirements of all life stages is important. While habitat preferences for most adult European Orthoptera, including the three analyzed species in this study (Cherrill and Brown 1990a; Hjermann and Ims 1996; Gottschalk 1997; Willott and Hassall 1998; Schuhmacher and Fartmann 2003; Hein et al. 2007; Schirmel et al. 2010a, b), are well understood, knowledge of egg and nymphal habitat requirements is rare or even lacking for many species (Detzel 1998; Ingrisch and Köhler 1998). The requirements of eggs and nymphs are usually very specific (Oschmann 1973; Ingrisch 1979; Ingrisch and Boekholt 1983), often explaining the distribution of species in our landscapes (Ingrisch 1988). Eggs demand the main part of the life-time (Ingrisch and Köhler 1998) and are due the lack of mobility directly influenced by the oviposition site conditions. Main determinants for oviposition site selectivity are the occurrence of suitable oviposition substrates (e.g. bare ground) and microclimatic conditions (moisture and temperature) (Ingrisch and Boekholt 1983; Ingrisch 1988). In contrast, nymphs are to some extent able to search actively for a suitable environment (van Wingerden et al. 1991; Gottschalk 1997; Ingrisch and Köhler 1998). Habitat quality in nymphs is mainly determined by vegetation structure (Cherrill and Brown 1992; Schuhmacher and Fartmann 2003) and microclimate (Lensink 1963). Predation and food availability are partly interrelated with the aforementioned parameters and usually also play an important role (Cherrill and Brown 1992; Gottschalk 1997). The great majority of dune and heathland Orthoptera require during the egg and nymphal period a dry and warm microclimate (Cherrill and Brown 1992; Ingrisch and Köhler 1998; Willott and Hassall 1998).

In order to improve our knowledge on the oviposition and nymphal habitat preferences of the three target Orthoptera species, we conducted a combined study consisting of a field survey and an outdoor experiment in summer 2009. Field work was done in a coastal heathland on the Baltic Isle of Hiddensee, Germany, where we analyzed nymphal habitat preferences. The outdoor experiment aimed to detect oviposition preferences of adult females. Therefore females were offered three different oviposition substrates (bare ground, mosses, lichens) imitating the main development stages of grey dunes in the heathland area (conducted at the Biological Station of Hiddensee). The following research questions were adressed: (1) What are the nymphal habitat preferences of the three species in the heathland? (2) Which substrates (bare ground, moss, lichens) are preferred for oviposition? (3) What can be concluded for species conservation and for practical management of dunes and heathlands?

Materials and methods

Study species

Myrmeleotettix maculatus (Thunberg 1815) (Caelifera: Acrididae)

Myrmeleotettix maculatus is among the smallest European Acrididae (size: 11–17 mm; Bellmann 2006) and specialized to open and sparsely vegetated habitats (Detzel 1998). Especially in dry sandy habitats the species can reach high densities and can be the dominant Orthoptera species (Ingrisch and Köhler 1998; Schirmel et al. 2010b). Egg pods (2–8 eggs) are placed shallowly into the ground and nymphs hatch in the following year (April/May).

Decticus verrucivorus (Linnaeus, 1758) (Ensifera: Tettigoniidae)

The 'wart-biter' *D. verrucivorus* reaches a size of about 4 cm and belongs to the biggest Orthoptera in Western and Central Europe (Bellmann 2006). In the northern European part of its distribution *D. verrucivorus* typically occurs in open and heterogenous dry grassland (Cherrill and Brown 1990b; Hjermann and Ims 1996; Schuhmacher and Fartmann 2003). Eggs are layed singly or in small groups into the soil (Ingrisch and Boekholt 1983; Cherrill and Brown 1990a) and development takes 2–8 years (Ingrisch 1986).

Platycleis albopunctata (Goeze, 1778) (Ensifera: Tettigoniidae)

The medium-sized *P. albopunctata* (about 20–28 mm, Bellmann 2006) occurrs mainly in open but heterogeneously vegetated habitats (Detzel 1998). In Northern

Germany and Europe it is often a rare species of dune ecosystems (Haes and Harding 1997; Kleukers et al. 1997; Maas et al. 2002). According to Gottschalk (1997) eggs are placed singly or in small groups mainly into the soil, in mosses or above ground into dead plant material (seed stands, wood). First nymphs hatch from April on in the following year (Ingrisch 1986).

Oviposition experiment

The oviposition experiment was conducted at the Biological Station Hiddensee (Fig. 1a; cf. similar experiments by Cherrill et al. 1991; Ingrisch and Boekholt 1983). In order to imitate natural conditions as well as possible, we conducted the experiment outdoors and with original substrate material from the heathland area where nymphal sampling took place. A wooden case (122 × 320 cm; 20 cm in height) was divided into 55 small (10 × 30 cm) and 16 large (20 × 30 cm) boxes covered by gauze. Each box was divided into three compartments filled with (1) sandy bare ground (in the following referred to 'bare ground'), (2) a moss carpet of *Campylopus introflexus* ('moss') and (3) different lichens of the genus *Cladonia* ('lichen') representing the main grey dune vegetation types in the study area and being the potential oviposition substrates (based on literature and our results from nymphal sampling). A pair of each species was kept between 29 June and 12 August within a box resulting in 38 replicates of pairs of *M. maculatus* (small boxes), 16 replicates for *D. verrucivorus* (large boxes) and 17 replicates for *P. albopunctata* (small boxes). Individuals were caught as nymphs or freshly hatched adults in the heathland area. The feeding took place in regular intervals using fresh herbs, grasses, oat flakes, and pieces of apple and cucumber distributed equally on the surface of each compartment. After release of the individuals, each compartment was searched for eggs or egg pods up to a depth of ~5 cm.

Nymphal sampling

Field work was conducted in a coastal dune heathland on the Baltic Sea island of Hiddensee, Germany (54°32′ N, 13°5′ E; Fig. 1a). The average annual precipitation is 547 mm and the average annual temperature 7.5°C (Reinhard 1962). The anthropo-zoogenic heathland is characterized by a small-scale mosaic of different types of dune and heath vegetation. The extensive dwarf-shrub stands are dominated by *Calluna vulgaris* (L.) Hull and *Empetrum nigrum* L. s. str., while *Corynephorus canescens* (L.) P. Beauv., *Carex arenaria* L. and *Cladonia* spp. dominate the grey dune vegetation. Nowadays, the landscape is kept open by clearing shrubs, sod cutting, mowing and sheep grazing.

As potential nymphal habitats of the studied species, four different vegetation types representing a gradient in vegetation density from intitial grey dunes to dwarf-shrub heath were chosen: (1) initial stages of grey dunes rich in bare ground, (2) grey dunes dominated by the invasive moss *C. introflexus* (Hedw.) Brid, (3) mature lichen-rich grey dunes and (4) homogeneous dwarf-shrub heath stands. Microhabitats of nymphs were recorded in an early (19 April–21 May) and a late (02 June–24 June) period in ten plots per vegetation type. Plots had a size of 25 m² (5 × 5 m) and were plane or had a slight southern aspect (<5°; S, SW, SE). Plots were divided into sub-plots (1 × 1 m) and presence-absence data of nymphs were recorded for nine sub-plots per plot (Fig. 1b). Microhabitat parameters were recorded in 60 × 60 cm around the perch location. In case of absence of nymphs within a sub-plot, reference data was collected at a randomly chosen location of the sub-plot. The selection of the random point was performed by a randomly thrown stick (Anthes et al. 2003). We recorded the following parameters: species, nymphal stage, cover (%) and height (cm) of heath, herbs, litter, lichens, mosses, proportion (%) of bare ground and vegetation density in the heights 0–10, 10–20, and 20–30 cm according to Sundermeier (1998). Vegetation was sampled in five randomly chosen sub-plots (1 m²) per plot.

Determination of species and nymphal stages follows Ingrisch (1977) and Oschmann (1969); nomenclature is based upon Coray and Lehmann (1998).

Statistical analysis

Differences in vegetation paramaters among vegetation types and the results of the oviposition experiment were analyzed using non-parametric Kruskal–Wallis H tests, as data did not meet ANOVA assumptions. Differences in egg/pod numbers between oviposition substrates were tested using Dunn's test as a post-hoc test at $P < 0.05$.

Differences in frequencies were tested using Chi^2 test. To determine the impact of the different environmental parameters within each of the four vegetation types on the occurrence of nymphs binomial generalized linear models (GLM) were conducted. For old nymphs (L3–L4) of *M. maculatus* sample size was sufficient to apply a separate GLM for each vegetation type. For the first instars (*M. maculatus*: L1–L2, *P. albopunctata:* L1–L3) data quantity was satisfactory for initial grey dunes and grey dunes dominated by mosses. In *M. maculatus* we additionally analyzed mature grey dunes. *D. verrucivorus* was generally omitted from the analyses, because of the small sample size. Intercorrelations of predictor variables were examined prior to GLM analysis by applying a Pearson's correlation matrix that included all metric predictor variables. Collinearity between predictor variables was
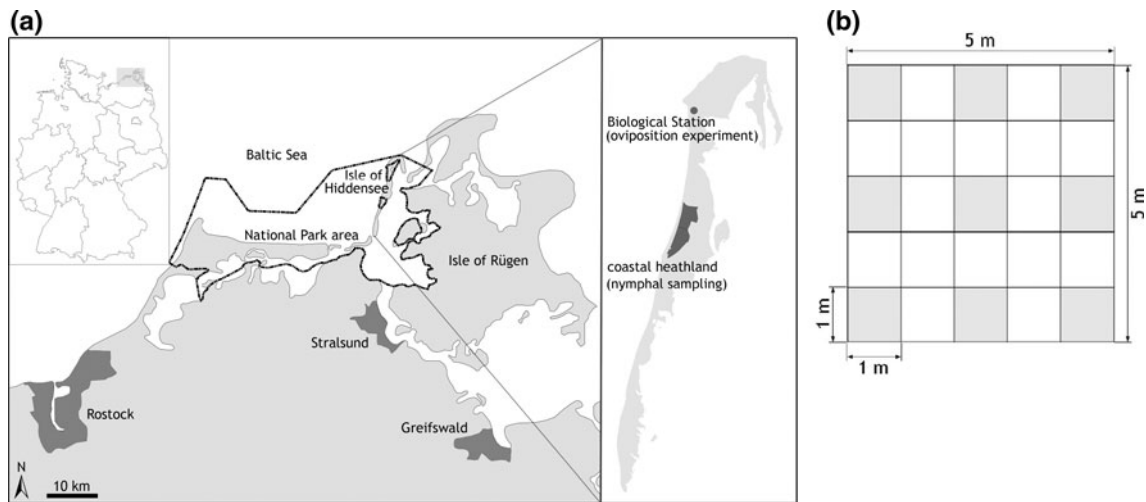
Fig. 1 a Position of the Baltic island of Hiddensee, of the coastal heathland (nymphal sampling) and of the Biological Station (oviposition experiment). b Plot-design for nymphal sampling. Search for nymphs was done in the nine sub-plots (*grey*)

generally low, with a Pearson correlation coefficient (r) of <|0.5| for all pairs except cover of lichens and height of lichens, cover of mosses and height of mosses as well as the density in the heights 0–10, 10–20, and 20–30 cm that were positviely correlated. To avoid problems associated with multicollinearity principal component analyses (PCA) were conducted to create a summarizing factor (cf. McCreadie et al. 2004; Stefanescu et al. 2004). The new variables present independent principal components hereafter called lichens, mosses and density. Their eigenvalues ranged from 1.7 to 2.6 and explained between 82.2 and 93.6% of total variance in the data sets.

All statistical analyses were done using R 2.10.1 (R Development Core Team 2009).

Results

Oviposition preferences

A total of 97 egg pods (median: 3.5 with 2.9 eggs per pod) of *M. maculatus*, 1,382 eggs of *D. verrucivorus* (median: 94), and 395 eggs of *P. albopunctata* (median: 6) were found in the offered oviposition substrates (Table 1). Eight of the 71 studied females (~11%) did not oviposit. Oviposition mostly occurred in more than one substrate.

The majority of pods layed by *M. maculatus* females were placed into bare ground (75%) followed by moss (23%) and under lichens (2% of eggs) (Fig. 2). The number of egg pods differed significantly among the three substrates. Twelve of the ovipositing females exclusively used bare ground as deposition substrate, two of them were

restricted to moss, whereas 13 of them completely avoided oviposition into moss.

Females of *D. verrucivorus* preferred moss (54%) and bare ground (46%) for oviposition (Fig. 2). The number of eggs under lichens was marginal and differed significantly from the other substrats.

Most eggs of *P. albopunctata* were found in moss (71%). The remaining eggs were found above ground at the branches of lichens (13%), in bare ground (12%) and above ground into the gauze (4%) (Fig. 2). Differences in egg numbers were significant among the four substrates.

### Nymphal-habitat preferences

All analyzed vegetation-structure variables differed significantly among the four vegetation types (Table 2). Initial grey dunes were characterized by a very high proportion of bare ground and some patches of herbs and grasses. Moss-rich grey dunes exhibited dense carpets of the invasive moss *C. introflexus*. One-fifth of the surface was covered by herbs and grasses. Mature grey dunes were dominated by lichens. The cover of herbs and grasses was slightly higher than in the two former vegetation types. Dwarf-shrub heath had by far the most dense vegetation. The proportion of bare ground as well as the cover of herbs/grasses and lichens was negligible.

We recorded 144 microhabitats and 174 reference plots for young nymphs of *M. maculatus* as well as 126 microhabitats and 156 reference samplings for old nymphs. Frequency of young and old nymphs significantly differed among the four vegetation types (Fig. 3). For young nymphs frequency decreased steadily along the vegetation density gradient from the initial grey dunes to the

Table 1 Summary of the results of the oviposition experiment

	Myrmeleotettix maculatus			*Decticus verrucivorus*			*Platycleis albopunctata*[a]		
Period of experiment	29.06.–11.08.2009			01.07.–12.08.2009			30.06.–12.08.2009		
No. of females	38			16			17		
Mean residence time (days)	30.3			34.9			29.7		
Females without oviposition	5			2			1		
Substrate:	Bare ground	Moss	Lichen	Bare ground	Moss	Lichen	Bare ground	Moss	Lichen
No of egg laying females	23	12	2	14	14	2	10	12	9
Total no of pods/eggs	78	17	2	634	744	4	49	279	50
Median (range) no of pods/eggs	3 (0–7)	0 (0–3)	0 (0–1)	40.5 (0–86)	52.5 (0–130)	0 (0–3)	1 (0–19)	3.5 (0–77)	1 (0–20)

[a] 5 females of *P. albopunctata* layed 17 eggs (median: 0, range: 0–8) above ground into the gauze
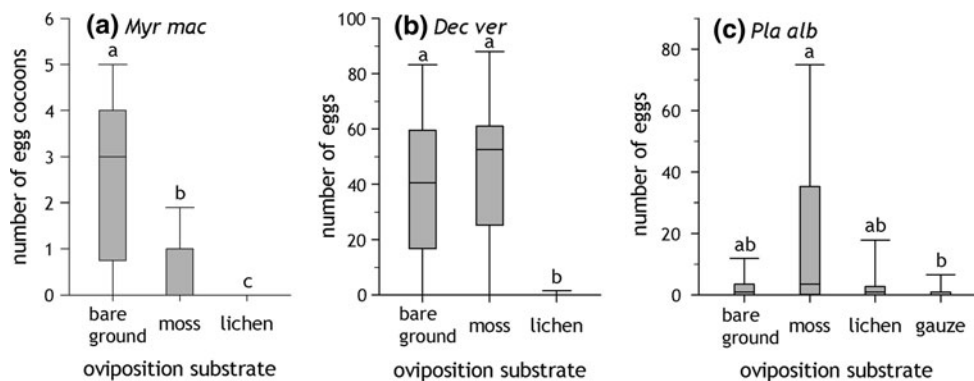
Fig. 2 Comparison of egg pod (*M. maculatus*)/egg numbers of the studied species between the offered oviposition substrates. **a** *M. maculatus* ($N = 38$; $H = 37.295$; $P \leq 0.001$). **b** *D. verrucivorus* ($N = 16$; $H = 24.400$; $P \leq 0.001$), **c** *P. albopunctata* ($N = 17$; $H = 10.366$; $P \leq 0.05$). Significance tested using Kruskal–Wallis H tests. *Different letters* indicate differences between groups (Dunn's test at $P < 0.05$). *Box plots* show 10th and 90th percentile (*whiskers*), 25th and 75th percentile (*boundary of the box*) and median (*line*)

Table 2 Vegetation structure of the four vegetation types with nymphal sampling

Parameter	ID	DM	MD	DH	H	P
Heath cover	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.5	80.6 ± 1.8	188.5	<0.001
Cover herbs	22.5 ± 1.3	18.0 ± 1.0	23.9 ± 1.3	2.1 ± 2.4	116.6	≤0.001
Height herbs	8.5 ± 0.4	10.4 ± 0.3	14.6 ± 0.5	8.7 ± 1.6	46.9	≤0.001
Cover litter	4.2 ± 0.3	5.5 ± 0.4	3.3 ± 0.3	16.9 ± 2.4	112.5	≤0.001
Proportion bare ground	70.6 ± 1.7	6.6 ± 1.1	3.9 ± 0.3	0.2 ± 0.2	167.6	≤0.001
Cover lichens	5.6 ± 1.4	8.1 ± 0.7	79.7 ± 1.3	2.1 ± 0.7	145.7	≤0.001
Height lichens	0.5 ± 0.1	1.5 ± 0.1	4.6 ± 0.2	0.5 ± 0.2	139.5	≤0.001
Cover mosses	2.1 ± 0.6	78.0 ± 1.3	4.6 ± 0.8	40.3 ± 3.9	151.4	≤0.001
Height mosses	0.2 ± 0.0	2.3 ± 0.1	1.1 ± 0.2	3.1 ± 0.2	115.6	≤0.001
Density 0–10	6.2 ± 0.8	6.3 ± 0.8	14.9 ± 1.4	63.1 ± 3.0	127.2	≤0.001
Density 10–20	0.3 ± 0.0	0.4 ± 0.1	1.5 ± 0.3	26.3 ± 2.7	123.9	≤0.001
Density 20–30	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	8.1 ± 1.6	105.3	≤0.001

Vegetation was sampled in five randomly chosen sub-plots (1 m^2) per plot. *ID* initial stages of grey dunes rich in bare ground, *DM* grey dunes dominated by the moss *C. introflexus*, *MD* mature lichen-rich grey dunes, *DH* homogeneous dwarf-shrub heath stands. Differences among vegetation types were analyzed using Kruskal–Wallis *H* tests
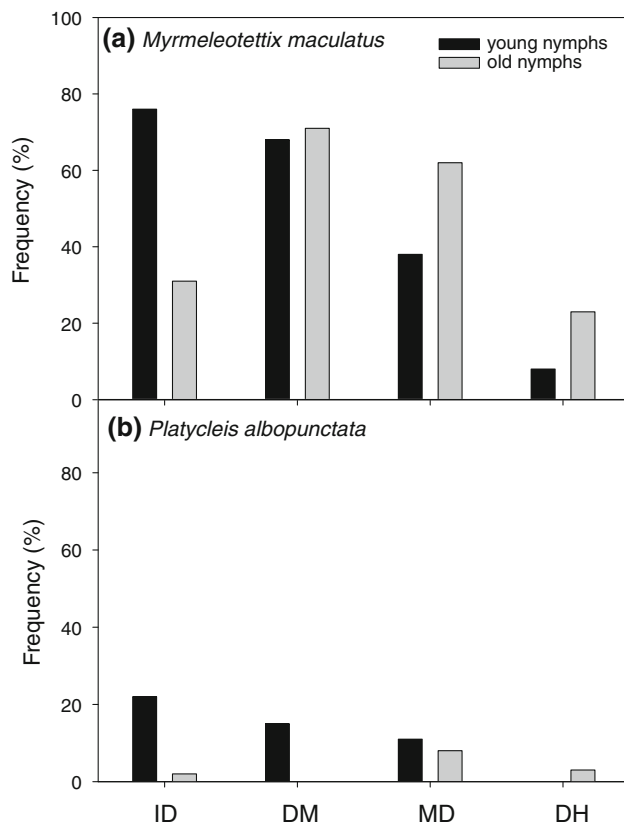
Fig. 3 Frequency of young and old nypmphs of **a** *M. maculatus* and **b** *P. albopunctata* in the four vegetation types with nymphal sampling. For abbreviations see Table 2. Differences in absolute frequencies of young and adult nymphs were analyzed using Chi^2 test. *M. maculatus*: $Chi^2 = 26.09$, $P \leq 0.001$; *P. albopunctata*: $Chi^2 = 19.31$, $P \leq 0.001$

dwarf-shrub heath. Except initial grey dunes, frequencies of old nymphs were in all vegetation types higher than those of young nymphs. Old nymphs were most frequent in moss-rich as well as in mature grey dunes. In initial grey dunes the likelihood of occurrence of both nymphal groups increased with vegetation density (Table 3). For old nymphs the cover/height of lichens was a further predictor and had a positive influence on the occurrence. In moss-rich grey dunes the occurrence of both nymphal groups was negatively correlated with the cover/height of mosses. Moreover, the likelihood of occurrence of old nymphs increased with the cover/height of lichens. In mature grey dunes presence of both nymphal groups was negatively associated with the cover/height of lichens. In dwarf-shrub heath old nymphs were more likely to be found with increasing proportion of bare ground and the cover/height of lichens.

For young nymphs of *P. albopunctata* 36 microhabitats and 108 reference plots were recorded and 10 microhabitats and 30 reference plots for old nymphs. As observed for *M. maculatus*, frequency of young and old nymphs of

P. albopunctata significantly differed among the four vegetation types (Fig. 3). For young nymphs frequency decreased from initial to mature grey dunes. In dwarf-shrub heath young nymphs were absent. In contrast, old nymphs were most frequent in mature grey dunes and dwarf-shrub heath. In initial grey dunes the likelihood of occurrence of young nymphs increased with the cover of litter and the height of herbs/grasses (Table 3). In moss-rich grey dunes occurrence of young nymphs was also positively correlated with the cover of litter. Moreover, the likelihood of occurrence decreased with the cover/height of lichens and mosses.

Discussion

Although the three umbrella species differed in the number of used oviposition substrates and their oviposition preferences, they shared the avoidance of lichens (= mature grey dunes) for egg-laying. The spatial resistance of the dense, highly branched, and under dry conditions very stiff cushions of *Cladonia* lichens hampers oviposition into the soil and very likely explains why the lichen treatment was so rarely used for oviposition. *Platycleis albopunctata* used the most different egg-laying substrates (four) without having a clear preference. Gottschalk (1997) also showed that the species is very flexible in its egg-laying substrate choice. However, he observed that most females laid their eggs in the field near the ground (e.g., in moss or rotten wood) or directly into the soil. In *Decticus verrucivorus* bare ground and mosses seem to be as important for oviposition while *Myrmeleotettix maculatus* clearly favoured bare ground. The special role of bare ground as an egg-laying substrate has already been document for the two species (*D. verrucivorus*: Ingrisch and Boekholt 1983; *M. maculatus*: Waloff 1950; Lensink 1963). That mosses can have a comparable relevance for oviposition in *D. verrucivorus* has so far been unknown. The higher air humidity above mosses (shown for *C. introflexus* in Schirmel et al. 2011) and their ability for water storage might even favour egg development of *D. verrucivorus*. Ensifera, even xerothermic species, need generally more water for egg development than Acrididae (Ingrisch and Köhler 1998) and the need of a sufficient water supply for development was demonstrated for *D. verrucivorus* (Moriaty 1970; Ingrisch 1988). Consequently, soils with moss carpets might be even more suitable oviposition habitats for *D. verrucivorus* than sandy soils without vegetation coverage. However, this assumption has to be tested in further studies.

Young nymphs of *M. maculatus* and *P. albopunctata* had similar preferences showing a decrease in frequency from initial to mature grey dunes and dwarf-shrub heath,

Table 3 Statistics of GLM: Relationship between occurrence of nymphs and environmental variables (predictor variable)

Response variable	Vegetation type	Explanatory variable	Estimate	SE	Z	P	R^2
Myrmeleotettix maculatus	ID						
Young nymphs		Density	22.786	9.085	2.508	<0.01	0.24
Old nymphs		Lichens	4.851	2.281	2.127	0.05	0.34
		Density	15.491	4.998	3.1	<0.001	
	DM						
Young nymphs		Mosses	–2.516	1.001	–2.514	<0.01	0.15
Old nymphs		Lichens	3.87	1.817	2.129	<0.05	0.19
		Mosses	–3.151	1.361	–2.316	<0.05	
	MD						
Young nymphs		Lichens	–2.804	0.760	–3.688	<0.001	0.41
Old nymphs		Lichens	–3.999	0.869	–4.601	<0.001	0.57
	DH						
Old nymphs		Proportion bare ground	0.163	0.091	1.794	<0.05	0.30
		Lichens	2.463	1.134	2.172	<0.05	
Platycleis albopunctata	ID						
Young nymphs		Cover litter	0.797	0.450	1.771	<0.05	0.47
		Height herbs	0.779	0.385	2.021	<0.05	
	DM						
Young nymphs		Lichens	–4.429	1.772	–2.499	<0.001	0.51
		Mosses	–3.147	1.707	–1.844	<0.05	
		Cover litter	0.737	0.403	1.828	<0.05	

Elimination of non-significant variables ($P > 0.05$) from the final model by stepwise backward-selection. P = P-value of likelihood ratio tests. For abbreviations see Table 2. R^2 = Nagelkerke's Pseudo R^2

respectively. Densities of young nymphs were also highest in initial and moss-rich grey dunes (Wünsch et al. 2011). Due to their restricted mobility young nymphs usually occur in close proximity to the oviposition sites (Lensink 1963; Cherrill and Brown 1992). Suitable egg-laying sites should comprise sufficient oviposition subtrates and favourable microclimatic conditions (see 'Introduction'). As shown in our oviposition experiment *P. albopunctata* is rather an oviposition subtrate opportunist than a specialist and hence, except in lichen-rich mature grey dunes, egg-laying substrate availability is hardly a limiting factor for this species. In contrast, *M. maculatus* strongly relies on bare ground for egg laying. However, both species have high temperature requirements in common (Willott and Hassall 1998; Gottschalk et al. 2003). In line with this, microclimate becomes cooler with increasing vegetation density along the gradient (cf. Stoutjesdijk and Barkman 1992) and the proportion of bare ground decreases.

While the frequency of young nymphs among the studied vegetation types particularly reflects the oviposition habitat requirements, the spatial distribution of the first instars within each type should also be attributed to the habitat demands of the nymphs. Within the grey dunes nymphs of *M. maculatus* and *P. albopunctata* preferred sub-plots with a higher/denser herbal layer or a higher litter

cover (only *P. albopunctata*). Moreover, occurrence in moss-rich and mature grey dunes was negatively correlated with the cover of the superabundant lichens and mosses. Open grey dunes are characterized by a warm microclimate (Schirmel et al. 2010a; Stoutjesdijk and Barkman 1992a, b) offering sufficient sites for basking. However, food availability might be low (cf. Gottschalk 1997). Although *P. albopunctata* is generally omnivorous (Ingrisch 1976), the early instars depend strongly on protein-rich nutrition, in particular flowers (Gottschalk 1997). *M. maculatus* feeds on grases and mosses (Zehm 1997). All these food resources are rare in the studied grey dune vegetation types, except mosses in moss-rich grey dunes. The herbal layer does not only provide food for the nymphs but also acts as a hidding site against adverse weather conditions (Lensink 1963) or predators (e.g., birds, lizards) (Cherrill and Brown 1992). The preference of *P. albopunctata* nymphs for a higher litter cover might be interpreted in the same way.

Although mature lichen-rich grey dunes are less important for oviposition and as a habitat for young nymphs, they are of high relevance for older, large-bodied nymphs. Both *M. maculatus* and *P. albopunctata* fulfilled a small-scale habitat shift from open initial/moss-rich grey dunes (young nymphs) to denser vegetated moss-rich and

mature grey dunes (old nymphs). Similar observations have already been made for *M. maculatus* (Lensink 1963) and *P. albopunctata* (Gottschalk 1997). *D. verrucivorus* is also known to shift its microhabitats (Cherrill and Brown 1992; Schuhmacher and Fartmann 2003).

Cherrill and Brown (1992) explained such microhabitat shifts during nymphal develompent as a strategy to avoid vertebrate predation. However, following Gottschalk (1997) the reasons for such shifts are more complex: microhabitat selection is a trade-off between favourable microclimatic conditions on the one hand and sufficient food and shelter on the other hand. Along the vegetation density gradient the former becomes more adverse, while the latter increases. The spatial distribution of old *M. maculatus* nymphs in the most open grey dune types (initial and moss-rich grey dune) underlines this assumption. Occurrence of nymphs was correlated with structures (dense vegetation, lichens) that can function as potential hiding sites. In contrast, dense dwarf-shrub heath provides sufficient shelter against predators. Here, occurrence seemed to be limited by the presence of warm sites for basking (bare ground, lichens).

Implications for conservation

Based on the results of this study, early seral stages of dune succession are crucial for the conservation of the three studied Orthoptera species. Bare ground and mosses represent keystone structures (sensu Tews et al. 2004) within the habitats. They were preferred as oviposition substrates, which is in accordance with the favoured habitats of young nymphs of *M. maculatus* and *P. albopunctata*, namely initial grey dunes with a high proportion of bare ground and moss-rich grey dunes. As studies by Cherrill and Brown (1992) for chalk grassland and by Schuhmacher and Fartmann (2003) for acidic grassland showed young nymphs of *D. verrucivorus* are also associated with patches of bare ground or short turf. Although *C. introflexus* carpets are important egg-laying substrates and nymphal habitats we have to mention that the moss is an invasive species in Europe and North America having negative impacts on plant diversity and vegetation (Ketner-Oostra and Sykora 2004, 2008; Hasse 2005, 2007) and on ground-dwelling arthropods (Schirmel 2011; Schirmel et al. 2011).

To allow successful development from the egg to the adult stage in all three xerothermic Orthoptera species habitat management has to preserve habitat mosaics of different successional stages in spatial vicinity (Schirmel et al. 2010b). Initial and moss-rich grey dunes play a major role for oviposition and as a habitat for young nymphs. In addition, old nymphs preferred the more densely vegetated moss-rich and lichen-rich grey dune vegetation. In

particular, adults of *P. albopunctata* and *D. verrucivorus* also differ in their requirements from that of the nymphs. They depend on the adjacent dwarf-shrub heath as shelter, song posts or to find food (Schirmel et al. 2010b). Therefore the preservation of a mosaic-like pattern of different grey dune and dwarf-shrub vegetation should be an aim of practical dune and heathland management measures (Schirmel et al. 2010a, b). In this regard the moderate use of paths (e.g. by tourists) and the restoration of sand dynamics might be beneficial for the creation of open and disturbed patches (Bonte et al. 2003; Maes and Bonte 2006).

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