

# Ground beetles of the Baltic Sea coast in Schleswig-Holstein (northern Germany) – Impacts of environmental parameters and spatial use

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**Abstract:** Ground beetles of the Baltic Sea coast in Schleswig-Holstein (northern Germany) - impacts of environmental parameters and spatial use – The carabid assemblages of sandy and shingle beaches, open and wooded cliffs, and lagoons were investigated at 9 locations on the Baltic Sea coast of Schleswig-Holstein in 2009. Lagoons, primary dunes and open cliffs exhibited the highest species richness according to the results of the sample rarefaction method. Carabid assemblages of lagoons were separated from all other coastal habitats but exhibited no exclusive species when compared to mainland lakes. Sandy and shingle beaches were not significantly distinct in terms of the carabid fauna. Soil moisture, wood cover and soil pH were the most important factors for the variance of the coastal carabid community. All species of the beach used the whole gradient from sand to shingle soils. *Asaphidion pallipes*, *Nebria livida*, and *Bembidion stephensi* were found to demand specific mixtures of sand and silt/clay in the open cliff habitat.

*Brosicus cephalothus* was found in high densities in the upper zones of sandy beaches. The population size of a 150 m section of beach was approximately 150 specimens. Although exhibiting a slow speed of only 7.7 m per day, *B. cephalothus* occupied a large home-range of  $236.3 \pm 24.4 \text{ m}^2$  on average. The mean maximum distance within its home-range accounted for  $86.9 \pm 5.8 \text{ m}$ . The large home-range of *B. cephalothus* can be explained by the poor prey conditions of beach habitats.

## 1 Introduction

The Baltic Sea coast of Schleswig-Holstein (northern Germany) contains numerous different habitats: cliffs, beach barriers, lagoons with and without contact to the sea, salt marshes, and different types of beaches. In contrast to the North Sea, the Baltic Sea coasts are not influenced by tides but are greatly dominated by waves. Erosion beaches are characterised by shingle or boulder; accumulation beaches are dominated primarily by sand. Based on these environmental conditions, the total coastal habitat up to the drift line can be inhabited by terrestrial organisms.

The beaches on both coasts in Schleswig-Holstein are highly attractive to tourists for recreational purposes and water related sport activities. Schleswig-Holstein has recorded a growing number of guest-nights, reaching a high in 2009 with more than 5 million guest-nights ([www.statistik-nord.de](http://www.statistik-nord.de)). It has been predicted that the number of tourists will increase even further as the water temperature increases due to climate change (SCHUMACHER & STYBEL 2009). As a result of the intensive use of European beaches, heavy damage to plant and animal communities has been observed (LLEWELLYN & SHACKLEY 1996; DUGAN

et al. 2008; SCHIERDING et al. 2011). A number of coastal conservation areas has been established in many countries of the European Union because of these impacts. However, while many conservation areas seasonally protect the breeding or migrant birds, they do not take the habitat demands for invertebrates and flora into consideration (WESLAWSKI et al. 2000; VELOSO et al. 2008).

Although the coastal habitats of Germany were studied long ago (KNÜLLE 1952; HEYDEMANN 1967), most investigations in the past have concentrated on salt marshes (IRMLER & HEYDEMANN 1986; MEYER et al. 1997; IRMLER et al. 2002). This has also been true for the Baltic Sea coast, where salt marshes are rarer than sandy beaches (SCHLIEMANN 2007; HENNICKE 2007). A few studies of primary dunes exist (SCHAEFER 1970; HÖRSCHELMANN 1990, SCHMIDT 2002), but beaches and cliffs have never been studied. For this reason the present investigation studies coastal habitats that were previously unknown from an ecological perspective. The following three aspects have already been published using the material collected by the present investigation: spiders (Araneae) (VAHDER & IRMLER 2010),

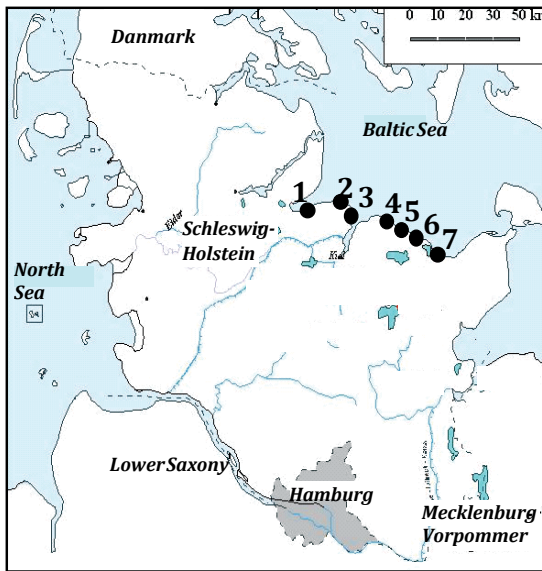


Fig. 1: The study sites at the Baltic Sea coast: Lindhöft (1), Dänisch-Nienhof (2), Stohl (3), Hohenfelde, Stakendorf (4), Huberstberg (5), Behrendsdorf, Lippe (6), Weißenhaus (7).

rove beetles (Staphylinidae) (IRMLER 2011) and the impacts of environmental parameters and tourism on the arthropod fauna and vegetation on beaches (SCHIERDING et al. 2011).

The present investigation describes the impact of environmental parameters and tourism on ground beetles (Carabidae). The goal of this study was to investigate the impact of soil conditions on ground beetles in regard to beaches and cliffs, since this impact has already been investigated in coastal dunes, coastal heaths and salt-marshes (IRMLER & GÜRLICH 2004). This study therefore mainly analyses the relation between soil and vegetation parameters and the oc-

currence of ground beetles on different beach and cliff habitats. Salt-marshes, dunes and heaths were intentionally omitted because detailed studies are already available (IRMLER et al. 2002; IRMLER & GÜRLICH 2004; SCHLIEMANN 2007; HENNICKE 2007). Additionally, the population ecology of *Broscus cephalotes* (L., 1758), which lives in the upper calcareous zone of beaches, beach barriers and primary dunes, was investigated in order to provide more information on the size of the population, mobility and home-range of beach animals.

## 2 Sites and methods

The investigations were performed in Schleswig-Holstein (northern Germany) on 9 beaches and cliffs at Lindhöft, Dänisch-Nienhof, Stohl, Hohenfelde, Stakendorf, Hubertsberg, Behrendsdorf, Lippe and Weißenhaus between 9.4.2009 and 20.8.2009 (Fig. 1). The beaches can be grouped into accumulative beaches such as lagoons, sandy beaches, shingle beaches and primary dunes, and erosive beaches such as open cliffs and wooded cliffs.

Cliff coasts develop at erosion coasts (SCHOTT 1956). They are exposed to high wave energy and typically develop fresh break-offs in the winter season, and have boulder and shingle beaches in front of the cliffs. The sedimentation coasts are exposed to lower wave energy than the cliff coasts and are characterised by sedimentation of fine-grained sand. At these coasts, lagoons that are partially or totally cut off from the sea sometimes develop behind sand barriers. On sedimentation coasts, different mixtures of shingle and sand on the beach are affected by different wave energies. High dunes like those found in the eastern Baltic Sea do not develop at Schleswig-Holstein's

Tab. 1: Number of pitfall traps in the investigated habitats of the 9 beach sections in Schleswig-Holstein.

Site (abbreviation)	Habitat (abbreviation)					
	Lagoon (L)	Primary dune (PD)	Sandy beach (SD)	Shingle beach (KS)	Open cliff (Su)	Wooded cliff (Sw)
Lindhöft (LH)	.	.	6	.	.	4
Dänisch-Nienhof (DN)	.	.	.	4	4	4
Stohl (ST)	.	.	.	6	4	.
Hohenfelde (HF)	4	4	8	.	.	.
Stakendorf (SD)	4	4	6	.	.	.
Hubertsberg (HB)	.	.	.	6	4	.
Behrendsdorf (BD)	4	.	6	.	.	.
Lippe (LI)	.	4	4	.	.	.
Weißenhaus (WH)	.	4	6	8	4	4

**Tab. 2:** Mean values of the determined soil and vegetation parameters in the investigated habitats. Different exponents indicate a significant difference with  $p < 0,05$  according to ANOVA.

Art	Wooded cliff	Open cliff	Lagoon	Sandy beach	Primary dune	Shingle beach
Soil moisture (%)	<sup>b</sup> 18 ± 3.0	<sup>c</sup> 8 ± 1.1	<sup>a</sup> 31 ± 5.9	<sup>d</sup> 1 ± 0.5	<sup>d</sup> 1 ± 0.5	<sup>d</sup> 1 ± 0.6
Wood	Yes	No	No	No	No	No
Sand content (%)	<sup>c</sup> 36 ± 6	<sup>b</sup> 46 ± 3	<sup>b</sup> 51 ± 16	<sup>a</sup> 89 ± 9	<sup>a</sup> 92 ± 9	<sup>c</sup> 22 ± 21
Shingle content (%)	<sup>c</sup> 5 ± 2	<sup>c</sup> 8 ± 2	<sup>b</sup> 21 ± 20	<sup>c</sup> 8 ± 10	<sup>c</sup> 6 ± 8	<sup>a</sup> 77 ± 20
Soil pH	<sup>b</sup> 7.4 ± 0.1	<sup>a</sup> 7.9 ± 0.2	<sup>b</sup> 7.5 ± 0.2	<sup>b</sup> 7.3 ± 0.2	<sup>c</sup> 7.2 ± 0.1	<sup>a</sup> 7.9 ± 0.3
Organic matter (%)	<sup>a</sup> 6.6 ± 2.6	<sup>b</sup> 1.1 ± 0.1	<sup>a</sup> 5.6 ± 0.9	<sup>b</sup> 0.2 ± 0.2	<sup>b</sup> 1.4 ± 2.2	<sup>b</sup> 0.3 ± 0.1

coasts. The number of coastal sections was selected in order to provide at least three sites per habitat type. Ground beetles were recorded by pitfall traps filled with 10% vinegar and a tension-reducing fluid. The pitfall traps had an opening of 5.6 cm diameter and were covered by a transparent shield to protect them from direct rainfall. A minimum of 4 pitfall traps per site were initially installed. However, because traps were sometimes destroyed by tourists, the number was increased to 8 pitfall traps shortly after the beginning of the study so as to guarantee that at least 4 traps per site remain intact. The total number of pitfall traps per site is listed in Table 1. Overall, 11 sampling intervals of two weeks each were carried out.

For each sampling interval, the water content of the soil was determined as the difference between fresh and dry soil (dried for 24 h at 110 °C). According to SCHLICHTING et al. (1995), content levels of shingle, sand and organic matter were determined once at the beginning of the survey: shingle content was determined by sieving a larger soil sample in the field; sand content was determined by sieving a soil sample using a 0.063 mm sieve after oxidising the organic matter with H<sub>2</sub>O<sub>2</sub>; finer silt and clay material was determined by subtracting sand content from the remaining soil weight; organic matter was determined after combustion of a dried soil sample; the pH-value was measured with a WTW-pH meter in 25 ml deionised water.

The investigations on *Brosicus cephalotes* were conducted in 2011 at the sandy beach of Behrendorf. In this area, tourists have access to the lower beach area but not to the backshore area or fore-dunes. On a 6 m wide beach section at a distance of 11 to 15 m from the shore, 153 individually marked pitfall traps were installed in three rows 3 m apart to allow an easy mapping of specimens to individual traps. To investigate the population size and movement behaviour, the mark-recapture method was applied (KREBS 1994) from 27.7.2011 to 21.9.2011. The specimens were

marked individually by milling the elytra (MÜHLENBERG 1993).

The statistical analyses were performed using the PAST programme (HAMMER et al. 2001). Normal distributed data were analysed using the one-factorial ANOVA with subsequent post-hoc test (Turkeys HSD-Test). Detrended Correspondence Analysis (DCA) was executed to ordinate carabid assemblages. According to ter Braak (1987), a distinct ordination of assemblages can be expected at eigenvalues higher than 0.5. To estimate the species richness of habitat types, the sample rarefaction method was employed. For the Canonical Correspondence Analysis (CCA), the Monte Carlo Permutation test was performed using the CANOCO programme to identify significant environmental parameters.

The population size of *Brosicus cephalotes* was estimated by the Jolly-Seber method (JOLLY 1965, SEBER 1965) using the Ecological Methodology programme (KREBS 1994). Furthermore, the mean daily movement distances were calculated from individual distances and time intervals of recaptured specimens. The minimum area method was used to estimate the home-range of individuals recaptured at least 5 times (ODUM & KUENZLER 1955).

### 3 Results

#### 3.1 Environmental parameters of the investigated habitat types

All habitat types were significantly differentiated by a specific combination of soil or vegetation cover parameters (Table 2). The sandy beaches and primary dunes had similarly high sand contents, but differed significantly in soil pH, with lower pH in the dunes and higher pH on the beaches. Both also had the lowest level of moisture and organic matter content. As expected, the shingle beaches had the highest shingle content, but also the highest soil pH at 7.9. Although

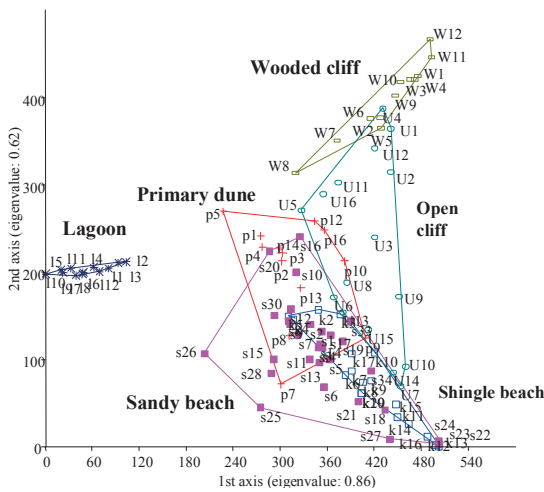


Fig. 2: Results of the Detrended Correspondence Analysis with sites and habitats: Lagoon (l), sandy beach (s), Shingle beach (k), Primary dune (p), wooded cliff (W), open cliff (U); digits indicate the individual pitfall traps.

shingle beaches had low sand content, soil moistures there were as low as those found on the sandy beaches and primary dunes. The lagoons were characterised by medium-high sand content, but exhibited the highest soil moisture, organic matter, and soil pH. Overall, the environmental conditions at lagoons showed the most balanced conditions of the investigated habitats. The two cliff coast types were differentiated by woodland or open conditions and also differed in soil pH and organic matter in the soil. The open cliffs had high soil pH, similar to that of the shingle beaches. The soil pH in both habitats was significantly higher than in all other habitat types.

### 3.2 Species composition

In total, 3185 specimens of ground beetles and 102

species were recorded (Appendix table). The number of species in the individual coast sections ranged from 18 to 51 (Table 3). The sections differed in their number of pitfall traps and habitats, however, which makes a direct comparison impossible. Comparing the habitat types, primary dunes and open cliffs showed the highest total species richness. Using the species richness per trap values, the lagoons exhibited the highest species richness. As the rarefaction method is best suited to compare habitats with different numbers of pitfall traps, this value showed the most realistic relationships between the habitats. According to the sample rarefaction method, the species richness at lagoons, on primary dunes and open cliffs are similarly high, whereas the wooded cliffs have the lowest species richness. Beach types, i.e. shingle and sandy beach, had intermediate species richness. A significant relationship between shingle or sand content and species richness for the beach habitats could not be found.

### 3.2 Species assemblages

According to the Detrended Correspondence Analysis (DCA), the species assemblage of the three lagoons showed the weakest similarity to beaches and cliffs (Fig. 2). Therefore, the first axis seemed to reflect the influence of the sea; lagoons located behind the beach barrier were least exposed to the sea. The second axis described the separation of open beach habitats via intermediate open cliffs covered by low vegetation to cliffs with wood. According to the results of the CCA-analysis, 4 parameters had a significant impact and explained 16 % of the total variance: soil moisture (eigenvalue: 0.29; F: 4.4), wood cover (eigenvalue: 0.50, F: 4.5), soil pH (eigenvalue: 0.29, F: 2.7), and shingle content (eigenvalue: 0.22, F: 2.1) (Table 5). For the remaining parameters, i.e. sand content and

Tab. 3: Species richness of ground beetles in the individual beach sections and habitats; 1 Sample Rarefaction refers to 12 pitfall traps.

Habitat type	Site									Species richness			
	BD	DN	HF	HB	LI	LH	SD	ST	WH	Total	per trap	<sup>1</sup> Rarefaction	RL
Lagoon	21	.	26	.	.	.	22	.	.	40	12.2±2.4	42.0±3.8	7
Sandy beach	11	.	16	.	4	11	11	.	16	42	3.9±1.9	23.8±2.7	9
Shingle beach	.	11	16	19	.	.	.	6	5	25	4.5±2.2	20.0±3.6	5
Primary dune	.	.	20	.	13	.	22	.	19	49	7.0±3.7	43.6±4.4	12
Open cliff	.	26	.	24	.	.	.	19	19	48	10.3±3.4	43.7±4.3	8
Wooded cliff	.	6	.	.	.	12	.	.	8	16	4.8±1.8	17.2±3.4	1

Tab. 4: Mean dominance (% in habitat) of most frequent ground beetles in the 6 types of habitats at the Baltic Sea coast.

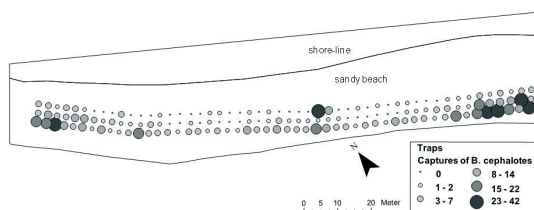
Arten	Lagoon	Primary dune	Sandy beach	Shingle beach	Open cliff	Wooded cliff
<i>Agonum thoreyi</i>	53.8	.	.	.	.	.
<i>Agonum afrum</i>	40.2	.	.	.	.	.
<i>Pterostichus strenuus</i>	8.1	.	.	.	.	.
<i>Bembidion assimile</i>	3.6	.	.	.	.	.
<i>Bembidion guttula</i>	2.8	.	.	.	.	.
<i>Oodes belopioides</i>	1.8	.	.	.	.	.
<i>Pterostichus nigrita</i>	21.2	4.3	3.2	1.4	9.8	.
<i>Dyschirius globosus</i>	15.5	4.2	3.6	1.7	1.4	.
<i>Carabus granulatus</i>	17.6	4.9	11.5	1.5	2.2	3.7
<i>Bembidion fumigatum</i>	1.9	3.5	.	.	.	.
<i>Ophonus puncticeps</i>	0.3	6.0	.	.	.	.
<i>Harpalus griseus</i>	.	3.5	.	.	.	.
<i>Amara fulva</i>	.	15.9	3.4	.	.	.
<i>Amara spreta</i>	.	10.2	5.1	.	.	.
<i>Demetrias monostigma</i>	.	9.3	7.2	.	.	.
<i>Bembidion pallidipenne</i>	.	3.8	5.2	.	.	.
<i>Dyschirius obscurus</i>	.	3.8	15.7	.	.	.
<i>Amara aenea</i>	.	.	4.0	.	.	.
<i>Amara convexiuscula</i>	.	.	2.8	.	.	.
<i>Microlestes mintulus</i>	.	.	3.5	.	.	.
<i>Brosicus cephalotes</i>	.	28.8	20.3	41.1	45.0	.
<i>Calathus fuscipes</i>	.	31.8	.	1.5	3.2	7.9
<i>Bembidion saxatile</i>	.	5.6	6.6	18.8	.	.
<i>Bembidion stephensi</i>	.	.	.	16.6	21.0	.
<i>Nebria livida</i>	.	.	3.2	9.6	4.7	.
<i>Acupalpus meridianus</i>	.	.	.	.	1.3	.
<i>Agonum muelleri</i>	.	.	.	.	2.5	.
<i>Asaphidion pallipes</i>	.	.	.	.	4.4	.
<i>Cybrus caraboides</i>	.	.	.	1.5	1.5	3.2
<i>Leistus terminatus</i>	0.9	.	.	.	1.4	5.9
<i>Abax parallelepipedus</i>	.	.	.	1.5	16.4	72.1
<i>Carabus nemoralis</i>	.	.	4.3	.	28.9	70.5
<i>Carabus coriaceus</i>	.	2.2	.	2.5	9.3	44.6
<i>Carabus hortensis</i>	.	.	11.8	1.2	.	25.7
<i>Pterostichus niger</i>	13.0	23.8	19.3	11.4	26.4	34.8
<i>Trechus quadristriatus</i>	1.1	26.9	71.9	2.8	3.6	3.7
<i>Nebria brevicollis</i>	0.5	25.7	5.4	2.9	18.8	9.7
<i>Bembidion tetracolum</i>	0.6	9.0	27.7	59.5	29.5	.
<i>Notiophilus biguttatus</i>	.	16.9	2.0	2.2	11.8	26.2

**Tab. 5:** Explanation of all significant parameters on the total variance in the Canonical Correspondence Analyses (total) and explanation of the individual parameters included into the model.

Parameter (%)	Carabidae	Staphylinidae	Araneae
Total	16	43	46
Moisture	29	32	32
Wood	28	23	27
pH	17	21	13
Shingle	13		
Sum	87	76	72

content level of organic matter, no significant effect was found.

The lagoon assemblage was characterised by species that are usually found at lakes (Table 4). In addition to exclusive species of lake shores, e.g. *Agonum thoreyi* and *Oodes helopioides*, widely distributed hydrophilous species occurred in this habitat, e.g. *Pterostichus nigrita* and *Carabus granulatus*. As in salt marshes, halophilic species were not found at lagoon shores. Exclusive species were not recorded in primary dunes. Many species occurred in primary dunes as well as on sandy beaches, but seemed to prefer one habitat or the other. *Amara fulva* and *Amara spreta*



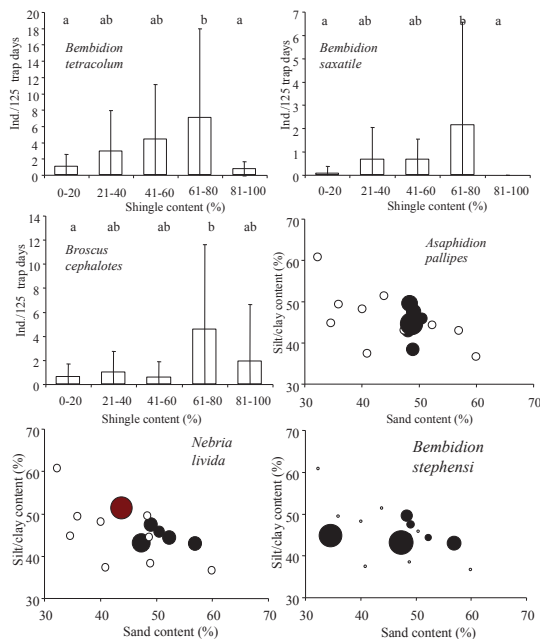
**Fig. 4:** Occurrence of *Broscus cephalotes* in the traps of a 6 x 150 m area at the sandy beach of Behrendorf.

were mainly found in primary dunes; *Bembidion pallidipenne* and *Dyschirius obscurus* mainly occurred on sandy beaches. *Amara convexisucula* was the only species found exclusively on sandy beaches. *Bembidion saxatile* was recorded on primary dunes, sandy beaches and shingle beaches; however, it was most frequently found on shingle beaches. Since the shingle beaches were located in front of open cliffs, some species were found on shingle beaches as well as open cliffs, e.g. *Bembidion stephensi* and *Nebria livida*. The three exclusive species, i.e. *Acupalpus meridianus*, *Agonum muelleri*, and *Asaphidion pallipes*, are also known from other open habitats with loam or clay soils, e.g. arable fields, where *B. stephensi* and *N. livida* are absent (IRMLER & GÜRLICH 2004). In wooded cliffs, which showed no exclusive species, only species that generally live in woods were found, e.g. *Abax parallelipedus* and *Leistus terminatus*.

### 3.4 Relationship between species and soil parameters

Since the beaches differ in shingle and sand content, the relationship between the shingle and sand mixture and the occurrence of species was analysed. Unfortunately, species that were expected to be characteristic of sandy beaches, e.g. *B. pallidipenne*, could not be analysed due to their rare occurrence. Among the species that seemed to prefer high shingle content, the three species *Bembidion tetracolum*, *B. saxatile*, and *Broscus cephalotes* were found numerous enough to execute a statistical analysis (Fig. 3). Highest numbers of individuals were found on beaches with a shingle content ranging between 60 % and 80 %. Lowest numbers were recorded on pure sandy beaches, but numbers were also low on pure shingle beaches.

Three species could be investigated in relationship to the mixture of sand and silt/clay of open cliffs. *Nebria livida* occurred in a range that was characterised by approximately 40 – 50 % of both sand and silt/



**Fig. 3:** Distribution of 6 ground beetles in the soil gradients; *Bembidion tetracolum*, *B. saxatile*, and *Broscus cephalotes* in the shingle – sand gradient of beaches; *Asaphidion pallipes*, *Nebria livida*, and *Bembidion stephensi* in the sand – silt/clay gradient of open cliffs; different characters indicate statistical differences with  $p < 0.05$  due to ANOVA; open circle: no record.

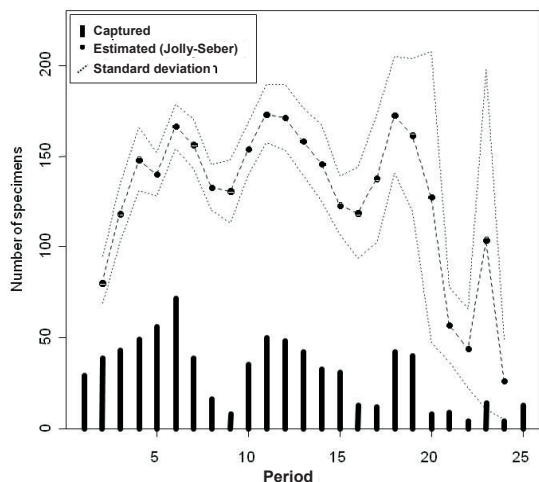


Fig. 5: Captures and population size of *Broscus cephalotes* during the study period from 27-June to 29-September, 2011.

clay. In contrast, *B. stephensi* was found in a range of 40 – 50 % silt/clay and a wide range of sand content, whereas *Asaphidion pallipes* occurred at a sand content of approximately 50 % and a wide range of silt/clay. Therefore, specific silt/clay content seemed to be of high importance for *B. stephensi*, whereas a specific sand content was more important than the silt/clay content for *A. pallipes*.

### 3.5 Population ecology and home-range of *Broscus cephalotes*

In total, 203 specimens of *B. cephalotes* were captured. The species was recorded over the entire investigated area but was significantly more frequent in the uppermost row of traps (Fig. 4). The total number of captures, including recaptures, amounted to 751 specimens. 443 specimens were captured in the uppermost row, 198 in the central row and 110 in the lowest row (ANOVA:  $F: 11.65, p < 0.001$ ). The estimated population size of *Broscus cephalotes* ranged from  $173 \pm 32$  specimens at mid-August to  $26 \pm 22$  specimens at end of September (Fig. 5). During summer, approximately one specimen of *B. cephalotes* can be expected per meter of beach. On average, a *B. cephalotes* specimen covered  $7.7 \pm 0.5 \text{ m day}^{-1}$ , but the data is heavily skewed ( $\gamma = 2.9$ ) and has a maximum of  $72.1 \text{ m day}^{-1}$ .

For the home-range, 66 individuals that were captured more than five times each could be analysed. The mean home-range of a *B. cephalotes* specimen covered  $236.3 \pm 24.4 \text{ m}^2$  on average, corresponding

to a maximum distance (within the polygon) of  $87.9 \pm 5.8 \text{ m}$  along the beach (Fig. 6). Unfortunately, a positive correlation to the frequency of recaptures was detected (Spearman-Correlation:  $\rho = 0.28, p < 0.05$ ).

## 4 Discussion

Spiders (VAHDER & IRMLER 2010), rove beetles (IRMLER 2011) and carabid beetles reflect different impacts of the coastal habitat conditions. In carabids, the low effect of environmental parameters on the assemblages becomes apparent when present results of ground beetle fauna are compared with that of staphylinids and spiders. This is not true for the differentiation along the first canonical axis that has an even higher value (0.83) than staphylinids and spiders (0.71 and 0.73). However, the impact of the environmental parameters on the staphylinid and spider assemblages was distinctly higher than on carabid assemblages (Table 5). Staphylinids and spiders seem to reflect the environmental variability of the coastal habitats to a greater extent than carabids. The sequential importance of the environmental parameters for the differentiation of assemblages was equal in all three groups. Overall, soil moisture was the most important factor, followed by wood cover and soil pH, whereas the shingle content exhibited a significant explanation only for carabids.

A further similarity between the three arthropod groups was found in the composition of the lagoon assemblage. Halophilic species that still occur in salt marshes of the Baltic Sea (REINKE et al. 2000; IRMLER et al. 2002) were not found in any of the three groups. High differences were found in the composition of the carabid, staphylinid and spider assemblages on beaches when specific preferences are considered. There were no exclusive carabid or spider species found for any beach habitat; whereas four staphylinid species occurred exclusively on sandy beaches. Furthermore, the differences between wooded and non-wooded cliffs were more distinct for staphylinids and spiders than for carabids. In particular, the staphylinids provided three species which demand specific mixtures of sand and silt/clay that were exclusive to the open cliffs. Although the similarities between the beach habitats, i.e. sandy beaches, shingle beaches and primary dunes, were high, the differences for staphylinids and spiders were more distinct than for carabids.

Large differences between the three groups can be ascertained with regard to species richness. For ground beetles, lowest species richness was found on

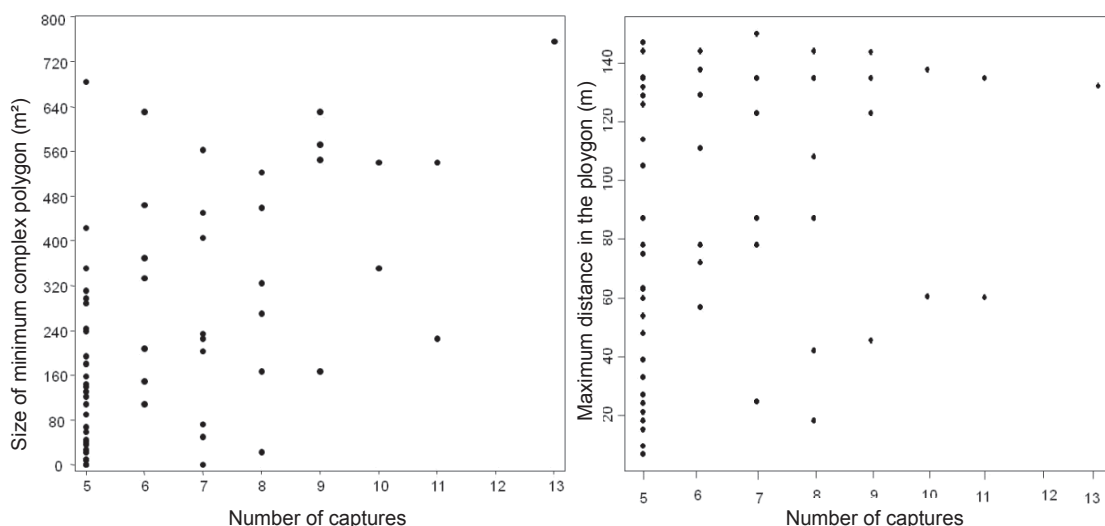


Fig. 6: Size and diameter of the home range (minimum complex polygon) of *Broscus cephalotes* for specimens with different number of recaptures.

sandy and shingle beaches. For staphylinids and spiders, shingle beaches accounted for the lowest species richness, as well, but sandy beaches had high or highest species richness. Staphylinid species richness was even higher at sandy beaches than at primary dunes, where spiders had the highest species richness.

The question now arises how the different reactions of the three groups can be explained. Beaches, particularly shingle beaches, are highly exposed to wind and wave energy (PECKHAM & WILLIS 1997). These habitats are very unstable compared to most mainland habitats. Species that have a long development time or low mobility can hardly adapt to such dynamic habitats. A decrease in species richness was found on unstable coastal habitats (KOTWICKI et al. 2005; JARAMILLO & MACLACHLAN 1993). In contrast to carabids, spiders and staphylinids are characterised by high mobility potential as they can either fly actively or exhibit ballooning behaviour. Furthermore, web-building spiders have an advantage in the primary dunes which have poor prey conditions, because they expend less energy for preying than the running carabids. Moreover, SCHIERDING et al. (2011) showed that, in contrast to staphylinids and spiders, species richness of carabids was equally high on closed beaches and on beaches open to tourists. The only species with higher abundance on beaches used by tourists, i.e. *B. tetracolum*, was found among the carabids. This can be explained by the fact that carabids provide no typical beach species or by the

theory that exclusive carabid species of beaches, e.g. *Cicindela maritima*, are nearly extinct and only widely distributed species, e.g. *B. tetracolum*, from frequently disturbed habitats, e.g. agricultural fields, remain.

*B. cephalotes* avoided the lower wrack zone and occurred significantly more often in the upper row of the examined beach section. According to IRMLER & GÜRLICH (2004), *B. cephalotes* prefers sandy calcareous habitats like upper beach zones or sandy agricultural fields. Beaches are characterised by low food densities for predators except in the wrack zone. The wrack zone, however, is extremely exposed to wind and waves and, therefore, unsuitable for long-living species like carabids. Activity measurements provide a suitable way to evaluate the home-range needed for food acquisition, e.g. for *B. cephalotes*. On sandy beaches, activity was already measured for the nearly extinct species, *Cicindela maritima* (IRMLER 2010). This species has an extraordinary flight activity and mobility with a speed of more than 100 m/h. The mean distance in its home-range was more than 50 m, which is high compared to home-ranges of carabids from woods, e.g. *Carabus problematicus* or *Abax parallelepipedus* with a mean distance of 14 m and 0.4 m. The fossorial species *B. cephalotes* exhibited a distinctly slower speed of 7.7 m per day. The speed of most other carabid species ranged between 0.2 m and 78 m per day (NIEHUES et al. 1996; CHARRIER et al. 1997; BAARS 1979; ASSMANN 1995; WALLIN & EKBOM 1988; SCHREINER & IRMLER 2010).



Only *Abax parallelepipedus* living in woods exhibits a lower speed of 0.2 to 0.6 m per day. In contrast to its low speed, the home-range of *B. cephalothes* is high at a distance of 90 m. Similarly high values were determined for *Cicindela maritima* from sandy beaches and *Carabus auronitens* in woods and *Poecilus versicolor* from heaths (NIEHUES et al. 1996; BAARS 1979). It can be assumed that the home-range is correlated to the availability of prey and must be high for predators living in habitats like sandy beaches which are low on prey. Whereas one specimen per 10 m beach section was determined for the strongly endangered *Cicindela maritima* (IRMLER 2010), the density for *B. cephalothes* was 10 times higher with one specimen per 1 m beach section. This means that a *Cicindela maritima* specimen cohabited its home-range with 5 other specimens, whereas 90 specimens of *B. cephalothes* used the same beach section. Therefore, the prey efficiency of *B. cephalothes* must be high and might be affected by a higher prey density in the soil compared to the density on the soil surface.

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**Appendix Table:** Activity density (trap per 125 days) of species of the investigated beach sections.

Art	Lindhöft	Dänisch-Nienhof	Stohl	Hohenfelde	Stakendorf	Hubertsberg	Behrens-dorf	Lippe	Weißenhäus
<i>Abax parallelepipedus</i>	2.1	3.7	.	.	.	.	.	.	1.86
<i>Acupalpus exiguus</i>	.	.	.	0.2	0.1	.	.	.	.
<i>Acupalpus meridianus</i>	.	.	0.1	.	.	.	.	.	.
<i>Agonum emarginatum</i>	.	.	.	11.3	7.8	.	.	.	.
<i>Agonum fuliginosum</i>	.	.	.	.	0.2	.	.	.	.
<i>Agonum muelleri</i>	.	.	0.2	.	.	0.1	.	.	.
<i>Agonum thoreyi</i>	.	.	.	20.0	18.6	.	15.2	.	.
<i>Amara aenea</i>	.	.	.	0.1	.	.	0.1	.	.
<i>Amara apricaria</i>	.	.	0.1	.	.	.	.	0.1	.
<i>Amara bifrons</i>	.	.	.	.	.	.	.	0.1	.
<i>Amara communis</i>	.	0.1	.	0.1	.	.	.	.	.
<i>Amara convexuscula</i>	.	.	.	0.2	.	.	.	.	.
<i>Amara familiaris</i>	.	.	.	0.2	0.1	0.2	.	.	.
<i>Amara fulva</i>	.	.	.	0.3	0.4	.	.	.	0.1
<i>Amara spreta</i>	.	.	.	0.7	0.1	.	.	0.1	.
<i>Anchomenus dorsalis</i>	0.1	0.9	.	.	0.1	.	.	.	.
<i>Asaphidion pallipes</i>	.	0.1	0.1	.	.	.	.	.	0.3
<i>Badister meridionalis</i>	.	.	.	0.2	.	0.1	0.1	0.3	.
<i>Badister peltatus</i>	.	.	.	.	0.1	.	.	.	.
<i>Badister sodalis</i>	.	.	.	.	0.1	.	.	.	.
<i>Bembidion assimile</i>	.	.	.	1.2	0.1	.	1.1	.	.
<i>Bembidion biguttatum</i>	.	.	.	0.1	.	.	.	.	.
<i>Bembidion femoratum</i>	.	.	.	.	.	0.1	.	.	.
<i>Bembidion fumigatum</i>	.	.	.	0.1	0.1	.	0.5	.	.
<i>Bembidion guttula</i>	.	.	.	.	0.1	.	0.5	.	.
<i>Bembidion illigeri</i>	.	.	.	.	0.1	.	.	.	.
<i>Bembidion lampros</i>	.	.	0.1	.	.	0.1	.	.	0.1
<i>Bembidion normannum</i>	.	.	.	.	.	.	.	.	0.1
<i>Bembidion obliquum</i>	.	.	.	0.5	.	.	0.1	.	.
<i>Bembidion pallidipenne</i>	.	.	.	.	0.3	.	.	.	.
<i>Bembidion properans</i>	.	.	.	0.1	0.1	0.1	0.1	.	.
<i>Bembidion quadrimaculatum</i>	0.1	.	.	.	0.1	0.1	0.2	.	0.1
<i>Bembidion saxatile</i>	.	.	.	0.1	0.1	0.7	0.2	.	0.2
<i>Bembidion stephensi</i>	.	.	0.2	.	.	2.7	.	.	0.2
<i>Bembidion tenellum</i>	.	.	.	.	.	0.1	0.1	.	.
<i>Bembidion tetracolum</i>	0.1	0.4	1.5	1.3	0.3	6.3	0.5	1.4	1.3
<i>Bembidion varium</i>	.	.	.	.	0.1	.	.	0.1	.
<i>Blemus discus</i>	.	.	.	0.1	0.1	.	.	.	0.1
<i>Blethisa multipunctata</i>	.	.	.	.	0.1	.	.	.	.
<i>Brosicus cephalotes</i>	1.1	0.7	13.0	0.8	0.6	2.5	0.3	0.7	1.5
<i>Calathus fuscipes</i>	0.1	.	.	2.6	0.1	0.2	.	.	0.1
<i>Calathus melanocephalus</i>	.	0.1	.	.	0.1	.	.	.	.
<i>Calathus rotundicollis</i>	.	0.1	.	.	.	.	.	.	0.1
<i>Carabus auratus</i>	.	0.1	.	.	0.1	0.1	.	0.1	.
<i>Carabus clathratus</i>	.	.	.	.	.	.	0.1	.	.
<i>Carabus convexus</i>	.	.	0.2	.	.	.	.	.	.
<i>Carabus coriaceus</i>	0.8	2.1	0.3	.	0.1	0.1	.	.	0.8
<i>Carabus granulatus</i>	0.1	.	0.3	0.3	5.0	.	2.4	0.4	0.1
<i>Carabus hortensis</i>	1.4	0.2	.	.	.	0.1	.	.	0.1
<i>Carabus nemoralis</i>	1.6	2.0	3.4	.	.	1.7	.	.	0.4
<i>Cicindela campestris</i>	.	.	.	.	.	0.1	.	.	.
<i>Clivina fossor</i>	.	.	.	.	0.2	.	.	.	0.1

Art	Lindhöft	Dänisch-Nienhof	Stohl	Hohenfelde	Staken-dorf	Huberts-berg	Behrens-dorf	Lippe	Weißenhau
<i>Cychrus caraboides</i>	0.1	0.1	.	.	.	0.1	.	.	.
<i>Demetrias monostigma</i>	.	.	.	.	0.1	.	.	0.1	0.3
<i>Dromius linearis</i>	.	0.1	0.1	.	.	0.1	.	.	0.3
<i>Dromius quadrimaculatus</i>	0.1	.	.	.	.	.	.	.	.
<i>Dyschirius aenus</i>	.	.	.	0.1	.	.	.	.	.
<i>Dyschirius globosus</i>	.	0.1	.	7.8	1.3	0.1	1.2	.	0.1
<i>Dyschirius obscurus</i>	.	.	.	.	0.6	.	0.1	.	.
<i>Elaphrus cupreus</i>	.	.	.	0.1	0.1	.	.	.	.
<i>Harpalus affinis</i>	.	0.1	.	1.4	.	0.50	0.2	.	0.1
<i>Harpalus griseus</i>	.	.	.	.	.	.	.	0.1	.
<i>Harpalus latus</i>	.	.	.	0.1	.	.	.	0.1	.
<i>Harpalus rubripes</i>	.	0.1	.	0.3	.	0.1	0.1	.	0.1
<i>Harpalus rufipes</i>	.	0.1	.	0.1	.	.	.	.	.
<i>Harpalus serripes</i>	.	.	.	0.1	.	.	.	.	.
<i>Harpalus tardus</i>	.	.	.	0.1	.	.	.	.	0.1
<i>Leistus rufomarginatus</i>	.	.	.	0.1	.	.	.	.	.
<i>Leistus terminatus</i>	0.1	0.1	.	0.2	.	.	0.1	.	.
<i>Limodromus assimilis</i>	.	0.1	.	.	0.4	0.1	.	.	.
<i>Loricera pilicornis</i>	.	0.1	0.1	0.1	0.1	.	0.1	0.1	.
<i>Masoreus wetterhali</i>	.	.	.	0.6	.	.	.	.	0.1
<i>Microlestes mintulus</i>	.	.	.	0.1	.	.	.	.	.
<i>Nebria brevicollis</i>	0.4	0.2	0.8	0.3	1.0	0.9	0.1	.	0.8
<i>Nebria livida</i>	0.1	0.2	2.3	.	.	0.4	.	.	0.1
<i>Notiophilus biguttatus</i>	0.1	0.1	.	.	.	0.8	.	0.3	0.9
<i>Notiophilus germinyi</i>	.	0.2	0.4	.	.	0.2	.	.	0.4
<i>Notiophilus palustris</i>	.	0.1	0.9	.	.	0.2	.	.	.
<i>Odacantha melanura</i>	.	.	.	0.1	0.3	.	.	.	.
<i>Omophron limbatum</i>	.	.	.	.	.	.	.	.	0.1
<i>Oodes helopioides</i>	.	.	.	0.1	0.3	.	0.1	.	.
<i>Ophonus puncticeps</i>	.	.	.	0.1	.	.	.	0.2	.
<i>Ophonus rufibarbis</i>	.	.	.	.	.	.	.	.	0.2
<i>Oxypselaphus obscurus</i>	.	.	.	0.8	0.1	.	0.1	.	.
<i>Philorhizus melanocephalus</i>	.	0.1	.	.	0.1	.	.	.	.
<i>Poecilus cupreus</i>	.	0.1	.	.	0.1	.	.	.	.
<i>Poecilus lepidus</i>	.	0.1	.	.	.	.	.	.	.
<i>Poecilus versicolor</i>	.	.	.	0.1	.	.	0.2	.	.
<i>Pterostichus diligens</i>	.	.	.	0.5	.	.	0.2	.	.
<i>Pterostichus gracilis</i>	.	.	.	.	.	.	.	.	0.1
<i>Pterostichus melanarius</i>	.	.	.	.	0.1	0.2	.	.	0.1
<i>Pterostichus minor</i>	.	.	.	.	0.2	.	.	.	.
<i>Pterostichus niger</i>	2.5	1.1	0.6	9.0	2.6	3.3	8.1	0.2	7.48
<i>Pterostichus nigrita</i>	.	0.1	.	1.7	5.0	0.4	0.2	0.2	.
<i>Pterostichus strenuus</i>	.	.	.	0.3	1.7	.	0.2	.	.
<i>Stenolophus mixtus</i>	.	.	.	0.4	0.1	.	.	0.1	.
<i>Syntoms foveatus</i>	.	.	.	.	.	.	.	.	0.1
<i>Syntomus truncatellus</i>	.	.	.	0.2	.	.	.	.	0.1
<i>Synuchus vivalis</i>	0.2	0.2	0.5	0.1	.	.	.	.	0.1
<i>Trechus quadristriatus</i>	.	0.3	.	8.7	0.3	0.2	1.1	0.1	0.4
<i>Trichocellus placidus</i>	.	.	.	0.1	.	.	.	.	.

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