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Autecology and population ecology of *Chlaenius nigricornis* (F., 1787) and *Blethisa multipunctata* Bonelli, 1810 in a wet grassland of northern Germany (Coleoptera: Carabidae)

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Summary

Chlaenius nigricornis and *Blethisa multipunctata* were investigated in a wet grassland area in Schleswig-Holstein (northern Germany) between 2005 and 2007. Autecological experiments in the laboratory revealed that water loss rates per hour were 2.2 for *B. multipunctata* and 3.2 for *C. nigricornis*. Both species preferred the wettest conditions in moisture gradient experiments and temperatures between 25°C and 30°C, but *B. multipunctata* showed a wider temperature range than *C. nigricornis*. In the field, *C. nigricornis* inhabited primarily sites with soil moistures between 30 % and 50 % and sites elevated between 30 cm and 50 cm above the water margin. It avoided sites with higher soil moistures and lower elevations, whereas *B. multipunctata* was only found directly at the water margin. The species were investigated in the field by the mark and recapture method using a close grid of pitfall traps. Both species had a first peak of population size at the end of April/first week of May and a second maximum in the first week of June, depending on weather conditions during the first time period. Seasonal records indicate that the larvae develop during two to three weeks in the second half of May. The population size varies between years, ranging between ~200 and ~400 individuals for *C. nigricornis* and ~100 and ~200 individuals for *B. multipunctata*. The population density was estimated to range between 0.06 ind. m^{-2} and 0.6 ind. m^{-2} for *B. multipunctata* and 0.1 ind. m^{-2} and 0.8 ind. m^{-2} for *C. nigricornis*. The median of mobility was calculated to be 1.5 m d^{-1} for *B. multipunctata* and 1.2 m d^{-1} for *C. nigricornis*; the corresponding values for home ranges were 44 m^2 and 19.7 m^2. Conservational aspects are discussed, including other ground beetle species of endangered wet grassland in northern Germany.

Keywords: wet grassland, ecological niche, mobility, home range, seasonality, population size

Zusammenfassung

Autökologie und Populationsökologie von *Chlaenius nirgicornis* (F., 1787) und *Blethisa multipunctata* Bonelli, 1810 in einem nassen Grünland Norddeutschlands (Coleoptera: Carabidae)

Die Laufkäferarten *Chlaenius nigricornis* und *Blethisa multipunctata* wurden in einem Feuchtgrünland in Schleswig-Holstein (Norddeutschland) in den Jahren von 2005 bis

2007 untersucht. Autökologische Experimente im Laborator ergaben, dass die Wasserverlustrate pro Stunde für *B. multipunctata* bei 2.2 und für *C. nigricornis* bei 3.2 lag; beide Arten bevorzugen im Experiment die feuchtesten Bedingungen des Feuchtegradienten und Temperaturen zwischen 25°C und 30°C. *B. multipunctata* nutzte einen weiteren Temperaturgradienten als *C. nigricornis*. Im Freiland besiedelte *C. nigricornis* hauptsächlich Standorte mit einer Bodenfeuchte zwischen 30 % und 50 % und solche die zwischen 30 cm und 50 cm über der Wasserlinie lagen. Die Art mied niedrigere oder nassere Standorte, während *B. multipunctata* nur direkt an der Wasserlinie vorkam. Die Arten wurden im Freiland mit der Markierungs- und Wiederfangmethode untersucht, wobei ein dichtes Netz von Bodenfallen eingerichtet wurde. Beide Arten hatten ihr erstes Aktivitätsmaximum Ende Apri/erste Woche im Mai und ein zweites Maximum in der erste bis zweiten Woche des Juni. Der Beginn der Aktivität hing von den Witterungsbedingungen während des ersten Aktivitätsmaxiums ab. Nach dem jahreszeitlichen Auftreten scheint es, dass die Larvalentwicklung während zwei bis drei Wochen in der zweiten Maihälfte stattfindet. Die Populationsgröße schwankte zwischen den Jahren. Sie lag zwischen ~200 bis ~400 Individuen bei *C. nigricornis* und ~100 bis ~200 Individuen bei *B. multipunctata*. Die Populationsdichte wurde auf 0,06 Ind. m^{-2} bis 0,6 Ind. m^{-2} für *B. multipunctata* bzw. 0,1 Ind. m^{-2} bis 0,8 Ind. m^{-2} für *C. nigricornis* geschätzt. Der Median für die Mobilität wurde mit 1.5 m d^{-1} für *B. multipunctata* und 1.2 m d^{-1} für *C. nigricornis* berechnet. Der entsprechende Wert für die Homeranges lag bei 44 m^2 und 19.7 m^2. Einnischung und Schutzaspekte werden diskutiert.

Schlüsselwörter: Feuchtgrünland, ökologische Nische, Mobilität, Homerange, Populationsgröße

Introduction

In northern Germany, wet grassland biotopes suffer under considerable environmental changes. On the one hand, in the past large areas were drained and fertilised to get additional pasture land of high economic value; on the other hand, recently wide areas have been abandoned, because agricultural use was no longer economical (IRMLER et al. 2010). According to SCHRAUTZER et al. (1996), 80 % of the wet grassland area in Schleswig-Holstein has been degenerated over the past 50 years. Only 5% of this land can be regarded to be oligotropic vegetation types with sparse vegetation cover that provide conditions for light demanding plant species. Therefore, oligotrophic wet grassland is highly endangered in northern Germany and shelters many endangered plant and animal species of Red Lists.

The endangered status of the wet grassland areas was the reason SCHREINER (2007) studied the ecological niches and population dynamics of ground beetles. She compared the endangered species *Elaphrus uliginosus,* which is restricted to wet grassland sites, with E. cupreus, which inhabits alder brooks and wet grassland. The present study aims to complete our knowledge about endangered ground beetles from wet grassland by studying the endangered species *Chlaenius nigricornis* (Red List status "3 - endangered") and Blethisa multipunctata (status "2 - critically endangered"). According to the investigations by Schreiner (2007), the ecological preferences of environmental conditions, e.g. temperature, moisture etc, the mobility determined by changing soil moistures, and the population size should be investigated. Focus was on the following questions: 1) How are the demands to soil moistures and temperatures? 2) How large is the home range and how mobile are the species? 3) How large is the population in the investigated area? 4)

Can we explain the distribution in the field by the ecological demands of the species? 5) How can the different use of wet grassland areas be explained?

Sites and methods

Site and ground species composition

The investigated site is located approximately 8 km south-west of Kiel (northern Germany, Schleswig-Holstein) in the large wet grassland area of the "Oberes Eidertal" near the village of Flintbek. The area is characterised by a moderate Atlantic climate. Thirty years average of both temperature and total yearly rainfall is 8.4°C and 874 mm, respectively (IRMLER et al. 2010). More details about the site and the "Oberes Eidertal" can be derived from IRMLER et al. (2010). In the years of investigation, the annual mean temperature was 9.5°C, 10.1°C and 10.2 in 2005, 2006 and 2007, respectively. During the period of study, the mean monthly average temperatures in April were colder in 2005 with 9.0°C and in 2006 with 7.6°C than in 2007 with 11.0°C. In May the temperatures of the three years were similarly high with 12.5°C in 2005, 13.0°C in 2006 and 13.5°C in 2007.

The investigated area is approximately 2200 m² large and part of a depression that developed after the last glacier time and covered a longitudinal flat projection of 1.1 ha area from a deeper and larger oval fen moor (Fig. 1). In the early spring, the investigated area is usually under water up to 0.5 m and becomes drier during spring and summer, whereas the fen moor is flooded throughout the whole year. While the investigated wet grassland is characterised by low peat layers and extensive cattle grazing during the growing season, the fen moor has very thick peat soils and cattle grazing is rarely found.

Fig. 1: Investigated site: a flat depression with astatic flooded area of approximately 2000 m² in the first half of May, when the water level has already decreased.

The two investigated species *Chlaenius nigricornis* (Fabricius, 1787) and *Blethisa multipunctata* (Linnaeus, 1758) inhabited the area together with several other ground beetle species, among them many other endangered species, e.g. *Elaphrus uliginosus* (Fabricius, 1792) and *Agonum viridicupreum* Goeze, 1777, which shows that the area is of great importance for natural conservation. Other frequent species were *Agonum viduum, A. fuliginosum, Carabus granulatus,* and *Pterostichus nigrita.*

Methods

Mobility and population dynamics methods

Chlaenius nigricornis was recorded in two selected areas of the study area: the one area most distant and the second area closest to the main fen moor. The species was collected by pitfall traps that were checked every second day to avoid loss by predation, drowning or starving. At the two sites, most distant and closest to the moor, 36 pitfall traps and 15 pitfall traps were installed, respectively. The most distant site was investigated in 2006 and 2007, the closest to the moor site only in 2007. The investigation period lasted from end of April to June. The specimens caught were marked by a drilling machine making flat impressions on different parts of the elytra (MÜHLENBERG 1993). More than 1000 specimens can be individually marked using this system. After marking, the specimens were released close to the trap in which they were caught. B. multipunctata was only found extremely close to the standing water margin. An investigation by pitfall traps was not possible due to danger of immerging. Therefore, this species was investigated by hand collection. The standing water margin was searched for *B. multipunctata* on the same days that pitfall change was performed for *Chlaenius*. The trampling effect was also used for *B. multipunctata*-collecting. Caught specimens were marked equivalent to *C. nigricornis* specimens. *B. multipunctata* was studied in 2005 and 2006 from April to June.

Autecological methods

Water loss was measured in a chamber above silica gel. Single specimens were sheltered into plastic boxes with openings that were put into the silica gel chamber for 180 to 200 min using 15 *C. nigricornis* and 14 *B. multipunctata* each. Water loss was determined as weight difference before and after the experiment. Relative air humidity was between 23 % and 25 % within the chamber.

Humidity preference was investigated in the laboratory under constant conditions of 20°C in a humidity gradient apparatus with 7 humidity levels ranging from 25 % to 80 % rel. air humidity. Humidity conditions were controlled during the experiments by an electronic humidity sensor. A similar experiment with 7 temperature levels was used to study the temperature preferences of the two species. Each preference experiment performed ten counts with ten species. After 20 min. of adaptation, the stops of specimens were counted every 10 min.

In addition to the experiments in the laboratory, field data were used to find preferences for soil moisture and vegetation parameters. A soil sample was taken every week to determine the soil moisture by the weight difference between moist and dried samples for this analysis. The soil samples were dried for 24 hr. at 110 °C. At beginning of May, for 1 m^2 around each pitfall trap the flooded area and the area of bare soil without vegetation was estimated. For the bare soil area, three groups were used: < 25 %, 26-50 % and larger 50 %. The flooded area around the traps was estimated in the groups: < 10 % and > 10 %. The relative elevation of each trap was also determined using a flexible tube level.

Statistical methods

The programs STATISTICA (STATSOFT 2004) and PAST (HAMMER et al. 2012) were used for statistical tests. Comparisons between groups were performed using either the Mann-Whitney U-test or the Kruskal-Wallis ANOVA with subsequent post hoc test using the Bonferroni correction. Sign test was used to test the temperature preference of both species. The seasonal trends of the two species were compared using the Wilcoxen-test. The same capture date was used as combining factor.

The population size was calculated using the Jolly-Seber method. This method can be used for open populations that are generally found in field investigations. The model demands at least 5 successive marking events. During the study period from end of April to mid of June, 14 marking events were conducted. The program Ecological Methodology was used for this calculation (KREBS 1999).

The home range was calculated for specimens caught at least three times. According to SOUTHWOOD & HENDERSON (2000), at least four recaptures are necessary for the calculation. They recommend combining the five points of captures of each specimen to calculate the area of home range. In the present investigation, no specimens of *B. multipunctata* and very few specimens of *C. nigricornis* were recaptured four times. When using the four points of the area used by a specimen, only vague values for the home ranges could be calculated.

Results

Autecology

Moisture and humidity

In the water loss experiment, rates of 2.21 ± 0.38 per hour for *Blethisa multipunctata* (14 trials) and 3.25 ± 0.85 per hour for *Chlaenius nigricornis* (15 trials) were identified. The data showed a non-normal distribution with a significant difference between the two species (z: -4.56, $p < 0.001$).

In the humidity preference experiment both species clearly preferred the chamber with the highest humidity of 75 % on average (Fig. 2). Only few specimens were found in the chambers with humidity lower than 50 %. No significant difference was found between the two species.

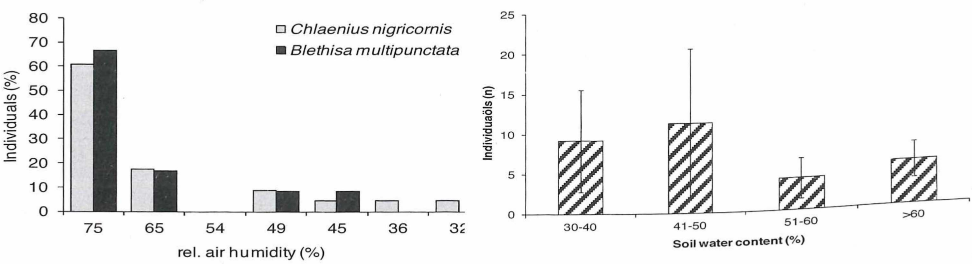

Fig. 2: Distribution of *Chlaenius nigricornis* and *Blethisa multipunctata* in the humidity gradient experiment (A) and of *Chlaenius nigricornis* in the soil moisture gradient in the field (B)

This result seems to be contradictory to the occurrence in the field. More specimens of *Chlaenius nigricornis* were recorded on soils that have between 30 % and 50 % soil moisture than on soils with moisture greater than 50 % (Fig. 2). The Kruskal-Wallis ANOVA found a significant difference between the four groups with H = 9.98 and p = 0.02. The post hoc test using the Bonferroni corrections showed that the two groups from 30 % to 50 % soil moisture differed significantly from the two groups with moistures higher than 51 %. As *Blethisa multipunctata* was always found directly at the water margin or even swimming on the water surface, it can be assumed that this species also preferred the highest soil moistures in the field.

Temperature preference

The temperature preference experiment exhibited a high temperature demand for both species (Fig. 3). They preferred a temperature range between 20°C and 30°C. Almost no specimens were found at temperatures lower than 20°C and higher than 30°C. This is particularly true for *Chlaenius nigricornis* that was only found between 20°C and 30°C and with the strongest preference for 26 - 29°C. The temperature range of *B. multipunctata* is wider, particularly in regard to the colder temperatures. Although the weighted means were very close with 25.4 °C for *C. nigricornis* and 24.8 °C for *B. multipunctata*, the comparison between the two species using the sign-test results in a significant difference of p = 0.04.

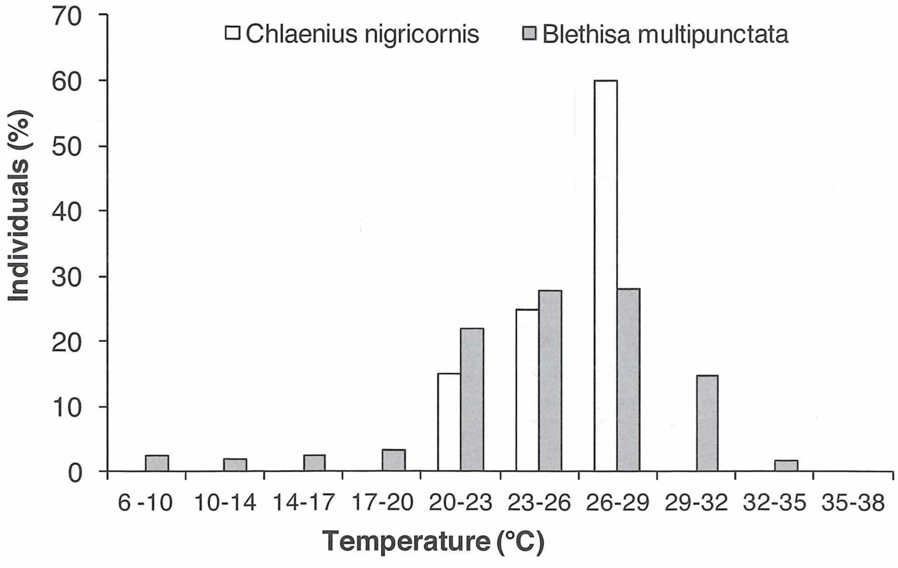

Fig. 3: Results of the temperature preference experiment for *C. nigricornis* and *B. multipunctata*.

Field parameters

The three field parameters, i.e. relative elevation, area free from vegetation and area covered by water, showed that *C. nigricornis* seemed to prefer the higher elevation within the studied area and avoided the area with dense cover of vegetation (Fig. 4). However, in regard to the elevation occurrence, the standard deviation was large and the differences between the groups were not significant (Chi^2 = 1.7, p = 0.6). The U-test between the two groups of water coverage also revealed no significant result. The comparison between the three groups of areas without vegetation revealed a weak significance. The pitfall traps in

> 50 % area free from vegetation had higher numbers of *C. nigricornis* than the pitfall traps with denser vegetation (Chi² 5.3 p =0.046, Bonferroni corrected pairwise comparison > 50 % different from groups < 50 % p = 0.01).

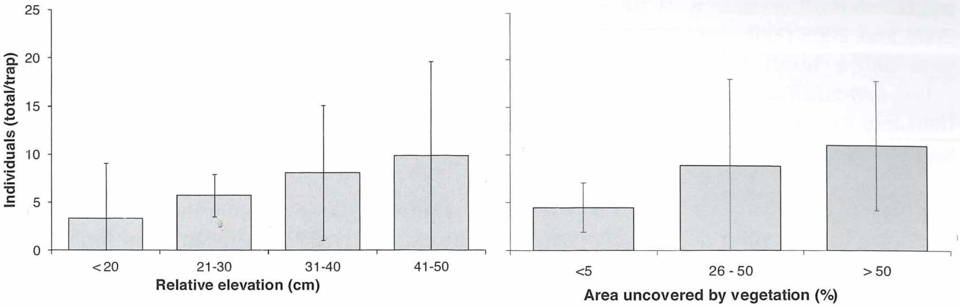

Fig. 4: Numbers of individuals/trap of *Chlaenius nigricornis* in pitfall traps of different elevation (left) and with areas uncovered by vegetation (right).

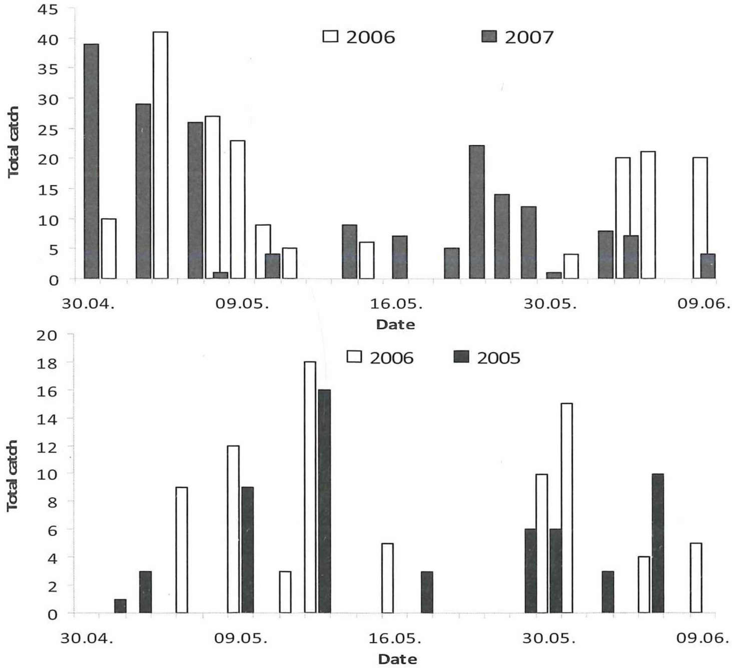

Fig. 5: Seasonal occurrence of *Chlaenius nigricornis* (upper graph) and *Blethisa multipunctata* (lower graph) during May/June of the years 2005, 2006, and 2007.

Population ecology

Seasonal dynamics

Both species showed high abundances and activities early in the year. High numbers of individuals were already caught at beginning of May (Fig. 5). Regarding the seasonal dynamics, *C. nigricornis* revealed highest values in the first two weeks of May. In 2005 and

2006 when there were lower temperatures at end of April/beginning of May, the early maximum was one week later than in the warmer period in 2007. During the two weeks following this peak, the species was seldom found. Higher catches were made once again at the beginning of June. In 2005 and 2006, this second peak was again 1 week later than in 2007. No differences were found for the population dynamics between the colder years 2005 and 2006 (Wilcoxen-test: p=0.16), whereas between 2005 and 2006 and the warmer year 2007 a significant difference was revealed (Wilcoxen-test: p=0.009).

For *B. multipunctata* a similar seasonal dynamic was found. Compared to *C. nigricornis*, the early maximum seemed to be one week later. As for *C. nigricornis*, the population dynamics for *B. multipunctata* did not differ between 2005 and 2006 (Wilcoxen-test: p=0.16).

Population size

The total investigated depression area was approximately 2000 m² with a circumference of 180 m. Since the investigation area was smaller in 2005 and 2006 (only the outermost area was investigated) than in 2007, the number of *C. nigricornis* catches was lower in these years (Table 1). The percentage of recaptured specimens in 2007 was higher than in 2005 and 2006. This had to do with the fact that during the study period of 2007 many specimens of the outermost area were recaptured in the innermost area. Thus, most *C. nigricornis* specimens used the total area of the investigated depression. Because *B. multipuncta* was caught in the total area, the marked and recaptured number of specimens refers to the total area. The percentage of recaptured *B. multipunctata* ranged between 18 % and 23 % and was distinctly lower than for *C. nigricornis*.

The population size seems to fluctuate distinctly in between the different years. For both species the total population size might differ at least for approximately 100 specimens.

Table 1: Number of captured and recaptured specimens of *Chlaenius nigricornis* and *Blethisa multipunctata* with calculation of the population size; confidence refers to 95 % interval.

	Chlaenius nigricornis			*Blethisa multipunctata*	
	2005	2006	2007	2005	2006
Total marked	63	146	275	51	66
Total recaptured	19	24	143	9	15
Recaptured (%)	31	16	52	18	23
mean population size	117	337	414	125	210
lower confidence	77	253	351	67	124
upper confidence	199	475	504	253	318

The density of the populations can only be roughly estimated due to the fact that the actual area used by the species can hardly be derived, because large areas of the depression were flooded deeply during a long period and could not be used by these species. Furthermore, the used area changed during the study period, because the water level decreased, moist area emerged and could be used by the species. At the beginning of May, the flooded area was 2000 m² large, at the end of the study period it was only 180 m² large. When *B. multipunctata* used a stripe of approximately 2 m adjacent to the flooded area, the density ranged between 0.06 ind m^{-2} and 0.10 ind. m^{-2} at the beginning of the investigation and between 0.3 ind. m^{-2} and 0.6 ind. m^{-2} at the end of the investigation.

As *C. nigricornis* is not as closely restricted to the water margin as *B. multipunctata*, a larger area might be used by this species. When *C. nigricornis* used 3 m adjacent to the water margin, the population density ranged between 0.1 ind. m^{-2} and 0.2 ind. m^{-2} at the beginning and 0.4 ind. m^{-2} and 0.8 ind. m^{-2} at the end of the study period.

Mobility and homerange

Most specimens of both species showed only a low mobility. Fifty to seventy percent of the specimens moved only about 1 m to 2 m per day (Fig. 6). During the entire study period, 60 % of *C. nigricornis* and 40 % of *B. multipunctata* moved less than 10 m. Overall, the mobility of *B. multipunctata* is slightly higher than that of *C. nigricornis*. More than 25 % of the *B. multipunctata* specimens moved more than 30 m during the study period. The corresponding value for *C. nigricornis* is less than 10 %. The median of moved distance was 1.5 m d^{-1} (lower quartile: 1.0 m d^{-1}; upper quartile 2.5 m d^{-1}; geometric mean 1.76 m d^{-1}) for *B. multipunctata*. The corresponding value for *C. nigricornis* was 1.2 m d^{-1} (lower quartile: 0.5 m d^{-1}; upper quartile 2.8 m d^{-1}; geometric mean 1.1 m d^{-1}). Even though it seems as if a larger part of the *B. multipunctata* population showed a higher mobility, the U-test revealed no significant results between the two species (U = 47, p = 0.83).

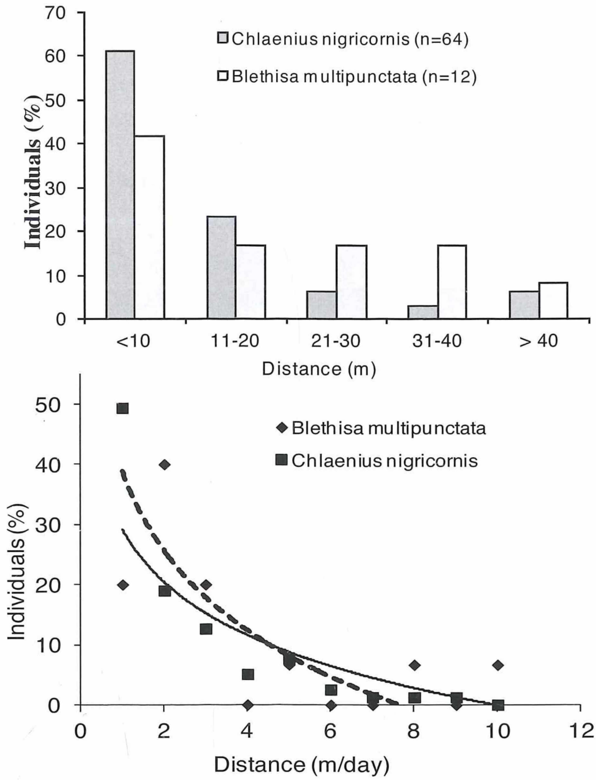

Fig. 6: Mobility of *Chlenius nigricornis* and *Blethisa multipunctata* showing the moved distance (m d^{-1}) (upper graph) and the total moved distance during the study period (lower graph).

The displacements of *Blethisa multipunctata* are shown in Fig. 7. The species apparently used the total flooded area. Although they are able to swim on the water surface, the species only used this way of movement when in danger. They crossed the area only after the immerging of most of the terrestrial area.

Only four specimens of *B. multipunctata* were recaptured a minimum of 3 times. Therefore, only a rough value for the home range, on average 44. 1 ± 39.9 m², could be calculated with a high range of confidence (95 %) values between 5 m² and 95 m². Sixteen specimens could be used to calculate the home range for *C. nigricornis*. The home range was 19.7 ± 25.2 m², with confidence (95 %) values of 6.2 m² and 33 m².

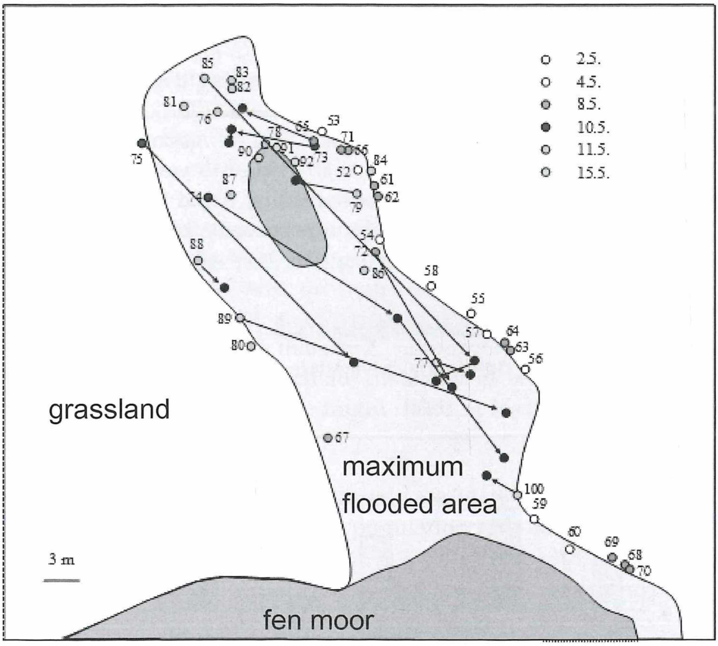

Fig. 7: Displacements of marked and recaptured *Blethisa* specimens during the study period. The light grey colour shows the flooded area at May, 2nd; the dark grey area at May, 15th. Arrows show the direction of movement.

Discussion

The two investigated species that were investigated, *C. nigricornis* and *B. multipunctata*, are part of a greater assemblage of ground beetles that are comprised of up to ten species. In contrast to the species investigated here, *E. cupreus* and *E. uliginosus* only inhabited restricted areas of the total area (SCHREINER 2007). These two species were investigated in detail by SCHREINER (2007), SCHREINER & IRMLER (2009) and SCHREINER & IRMLER (2010). Hence, a comprehensive comparison may be conducted with these species. Water loss of *E. cupreus* and *E. uliginosus* ranged between 1.5 % and 2 % per hour, which is considerably lower than the 2.2 % and 3.2 % per hour of *B. multipunctata* and *C. nigricornis*. Thus, these two species seem to be more dependent upon wet conditions than the two *Elaphrus* species. The moisture gradient experiment revealed no additional explanation about the impact of moisture conditions on the ecological demands. After several hours of experiments, all four species were most frequent under the wettest conditions. However, the females of the two *Elaphrus* species were significantly less dependent on moisture conditions than the males (SCHREINER & IRMLER 2009). According to KROGERUS (1960), the hemolymph of species preferring acidic, wet conditions is more acidic than those preferring alkaline, wet conditions such as *B. multipunctata*. This might be the reason these four species prefer alkaline conditions of groundwater near fen moors and why they are not found in acidic bogs.

In terms of the field measurements, both *Elaphrus* species inhabited soil moistures between 50 % and 70 % and were absent at sites with soil moistures less than 50 %. In contrast, at least *C. nigricornis* was found in higher numbers of individuals at sites having soil moistures lower than 50 %. According to THIELE (1977), who summarised the knowledge about ecological demands of carabids, moisture demands are independent from seasons but must be regarded as a combination of temperature and moisture demands. *Limodromus assimilis* rarely occurred in the investigated wet grassland because the species has low temperature demands. The low temperature demands might be the reason why this species primarily dwells at wet alder forests and rarely invades wet grassland (IRMLER & GÜRLICH 2004). With the exception of *E. cupreus,* the species investigated only occur in wet grassland. THIELE (1977) stated that species from wet habitats preferred moist conditions and those from dry habitats prefer dry conditions. Flooded areas are usually avoided, as found for the two *Elaphrus* species and *C. nigricornis*. The two *Elaphrus* species avoided sites with more than 25 % flooded area. The preferred elevation zone of *C. nigricornis* also showed that it avoids living directly at the water margin. In contrast, *B. multipunctata* is well adapted to an amphibious life. AHRENDS & BAUER (1987) found a well-developed diving behaviour for *B. multipunctata*. The species enters the water spontaneously and is able to stay beneath the surface for more than 1 hour without renewing its respiratory air.

More than 70 % of the investigated carabid species have a preferred temperature range of 15°C according to THIELE (1977). He stated that the preferred temperature plays a considerable role in the geographical and ecological distribution of carabids, but is not the most important response to microclimate. Of the four carabid species compared here, all four species preferred temperatures between 20°C to 35°C but *C. nigricornis* revealed the narrowest temperature range. The three other species used a wider range, from 10°C to 35°C. *E. cupreus,* which also inhabits wet alder woods, showed no preference for lower temperatures in comparison to the pure grassland dwellers. However, according to KROGERUS (1960), the Scandinavian *E. cupreus* preferred a mean temperature of 22.5°C, whereas the studied population here preferred temperatures between 25°C and 30°C. Therefore, populations from different climatic regions seem to differ in their temperature preferences.

In contrast to *B. multipunctata* and *C. nigricornis,* the two *Elaphrus* species inhabited highly restricted areas of the investigated wet grassland. The two species need moderately large areas free from vegetation for their predatory life, according to SCHREINER & IRMLER (2009). They found that the most important factor for the small scale distribution was the percentage of bare soil space without cover of vegetation. *E. cupreus* almost exclusively inhabited sites with a percentage of more than 25 % bare soil, whereas *E. uliginosus* could frequently be found at sites with 5 % bare soil. No information about the importance of vegetation-free areas is available for *B. multipunctata,* but *C. nigricornis* also seemed to prefer areas without vegetation cover.

Ecological demands of the species may explain their ecological niche and micro-restriction within their habitats (KLEINWÄCHTER & RICKFELDER 2007). The combination of moisture and high temperature demands of the species together with the demand for high alkaline soils can explain why they occur in the investigated area, but they cannot explain the micro-patchiness with different uses of the area. SCHREINER & IRMLER (2009, 2010) proposed three factors that separate the niches of *E. uliginosus* and *E. cupreus*. One is the demand for larger areas without vegetation cover by *E. cupreus*. Therefore, it usually inhabits alder woods without ground vegetation. The prey foraging of *E. cupreus* seems to be more effective than that of *E. uliginosus* when considering the longer diurnal activity. The restriction to the direct water margin by *B. multipunctata* cannot be explained by the factors investigated in the laboratory. It could be affected by the competition with the similarly large *C. nigricornis* or to the ecological demands of the larvae or the egg laying substrate, such as found for *P. melanarius* (TRÉFÁS & VAN LENTEREN 2004). Since *B. multipunctata* has developed a diving ability, it is able to use the direct water margin which is avoided by *C. nigricornis*. In addition, the use of a wider temperature range might be the reason *B. multipuncata* can use the direct water margin avoided by *C. nigricornis*. Unfortunately, nothing is known about the ecological demands of the larvae.

At river banks, carabid species have well-developed flight ability and high mobility to escape from flooding and to hibernate at sites that are not endangered by flooding in winter (ANDERSON 1968, BONN 2000). The species studied here also have well-developed flight ability and hibernate outside the described wet site (SCHREINER 2007). In contrast to adults, eggs seem to survive longer periods under flooded conditions (TAMM 1984, WEIGMANN & WOHLGEMUTH-VON REICHE 1999). According to MEISSNER (1983), riparian carabids do not walk directly between summer and hibernating sites, but rather seek their hibernating sites by flight. This mobility is needed for prey foraging and for moving along the retreating water level from beginning of May to mid-June. Compared to *C. nigricornis* and *B. multipunctata* with an average range of 1.2 m d^{-1} and 1.5 m d^{-1}, *E. cupreus* and *E. uliginosus* have considerably lower mobility. They only move 0.5 m d^{-1} and 0.7 m d^{-1}, on average (SCHREINER & IRMLER 2010). This may be why they utilize smaller areas than *C. nigricornis* and *B. multipunctata*. The two *Elaphrus* species only used an area between 135 m^2 and 440 m^2, whereas *C. nigricornis* and *B. multipunctata* used the entire area of approximately 2000 m^2. According to SCHREINER (2007), the *Elaphrus* species used their flight ability to cross wider distances between different populations of the valley.

Few investigations are available regarding the population size of carbid species. More information about the population size is needed in order to evaluate conservational priorities. SCHREINER (2007) studied 9 populations of the two *Elaphrus* species. The population size of the endangered *E. uliginosus* ranged between 22 and 210 individuals while the non-endangered *E. cupreus* between 11 and 583. However, the population size of *E. uliginosus* showed higher fluctuations at the investigated site, ranging between 32 and 210 individuals. Nevertheless, *E. uliginosus* never reached the high population size of more than 500 individuals, such as *E. cupreus* had attained under optimal conditions. Most populations accounted for no more than 30 individuals. In the investigated area, both *C. nigricornis* and *B. multipunctata* had larger populations than the two *Elaphrus* species, but also showed great fluctuations in their population size. However, the population size of the investigated area can be regarded as maximum sizes for these species when compared to the population size of *E. uliginosus.*

It can be stated that the investigated wet grassland offers optimal conditions for endangered species which depend on high soil moisture, open vegetation and alkaline soil conditions. Therefore, it is important to emphasise the most essential factors providing such optimal conditions for a number of endangered carabids. Certainly, wet conditions with astatic water level fluctuations offer the best conditions for species with different demands on wet soil moisture. The open grassland habitat within a sheltered landscape depression provides warm temperatures that are needed by all endangered species found there. Thirdly, grazing by cattle produces open, bare soil that is rapidly warmed up on sunny days in the spring and is a needed requisite for optically-foraging carabids. A grazing management of wet grassland is certainly more useful than a mowing management for these species, as is sometimes proposed by botanists for the conservation of wet grassland. However, comprehensive grazing management is needed to find a balance between the destructive effect of cattle trampling and the demanded bare soil areas for the carabids.

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