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Ecomorphological adaptations of riparian carabid beetles

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Summary

Carabid beetle composition, microhabitat preference in relation to soil texture and microclimate, and behavioural aspects such as diurnal and dispersal activities have been studied on river banks in the Belgian Famenne. The possibility of the occurrence of ecomorphological adaptations was also investigated by means of a biometric approach to body shape and hind wing development. Micromorphological adaptations are visible along three investigated ecological axes : (1°) differences in body shape can be related to the structure of the microhabitat, (2°) the degree of metallic coloration of the integument corresponds to the amount of activity during daytime and (3°) a well developed flight apparatus matches the unpredictable instability of the habitat of these species.

Key-words : carabid beetles, river banks, microhabitat preference, ecomorphology

Résumé

Adaptations écomorphologiques des Coléoptères carabiques rivulaires
La composition de la faune Carabidologique, la préférence des espèces du microhabitat en relation avec la texture du sol et du microclimat, ainsi que différents aspects de leur comportement (activité diurne et dispersion) ont été étudiés sur les rives de l'Ourthe situées dans la Famenne belge. La possibilité de l'existence d'adaptations écomorphologiques a également été étudiée à l'aide d'une approche biométrique de la forme du corps et du développement des ailes membraneuses.
Des adaptations sont décelables pour les trois axes écologiques étudiés : (1°) les différences observées de la forme du corps peuvent être mises en rapport avec la structure du microhabitat, (2°) le degré de coloration métallique de l'intégument correspond à la proportion de l'activité réalisée durant la journée et (3°) un appareil de vol bien développé chez ces espèces est conforme à l'instabilité imprévisible de l'habitat.

Mots-clefs : Coléoptères carabiques rivulaires, préférence du microhabitat, écomorphologie

Introduction

From 1985 onwards we have been studying the carabid fauna on river banks along the river Ourthe in the Belgian Famenne district. Different sampling techniques have been utilized in order to assess the abundance and population dynamics, microhabitat preference and diurnal activity of these beetles.
River banks can be divided into a great number of microhabitats differing in edaphic conditions and microclimate. The diversity of carabid species in riparian habitats as a rule is very high and, especially on coarse and stony river banks without vegetation, exceeds that of all other macro-invertebrates. This is partly due to the very large number of stenotopic species, especially belonging to the species rich genus *Bembidion,* which are restricted in their occurrence to these habitats. The study of carabids on river banks thus offers important possibilities for nature conservation applications. Besides the contribution to bio-indicator projects, these beetle communities pose a number of more fundamental questions to ecologists. These mainly concern the description and understanding of the species-specific microhabitat preferences and the study of the adaptive values associated to the ecophysiology and ecomorphology of the different species.
In this paper we will focuss on the last-mentioned aspect and restrict our analyses to 7 species of the genus *Bembidion.* We will compare some ecomorphological aspects of these most abundant *Bembidion* species encountered during our study. *Bembidion's* are small carabids : the species studied here vary in body length between 3.5 and 6 mm. First of all we will define and compare the microhabitat preference of these species in relation to the soil texture and microclimatological conditions on the substrate as possible cues related to their microhabitat choice. We will then investigate the possibility of the occurrence of ecomorphological adaptations, in part by means of a biometric approach to body shape and dispersal power. These adaptations will be searched for along three investigated axes : (1°) body shape in relation to microhabitat structure, (2°) coloration of the integument in relation to diurnal activity and (3°) hind wing and flight muscle development as a measure of the dispersal power in relation to the risk of inundation as a measure of habitat unpredictability. ANDERSEN (1985) already demonstrated a close relationship between body shape and ecology of some riparian species of the tribe Bembidiini in Norway. Most *Bembidion* species in our study however do not occur in Norway or where not included in Andersen's study. Hereafter, we will test his results and extend them to the other ecomorphological aspects mentioned.

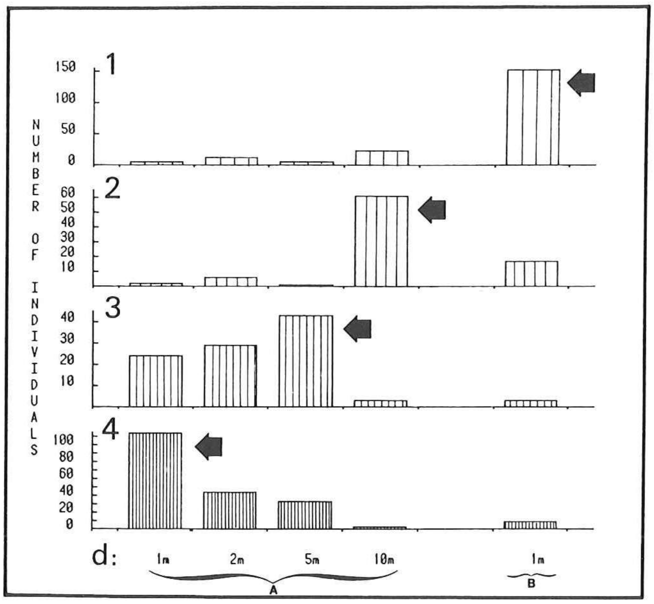
Material and methods

As already mentioned, different sampling techniques were utilized in our study. Absolute abundance estimates were made by means of a combined quadrat sampling - flottation technique, which was developed by us. The technique has already been described in detail in an earlier paper (DESENDER & SEGERS, 1985). Sampling mainly took place on two different river banks of the river Ourthe near the village Petite Eneille and was mostly performed at the end of June - beginning of July. On each occasion at least 30 sampling units of 40cmx40cm were taken. Abiotic characteristics (soil texture, coverage by larger stones, temperature and relative humidity on the soil surface) were noted and the exact location of the sampling unit sites mapped. Additional relative abundance estimates were obtained from hand catches per time unit of effort in different zones per sampling occasion. These were performed on 5 occasions by 6 to 13 persons simultaneously. Results from these samplings were analyzed by a Friedman-two way ANOVA, taking the dependency of results from individual catchers into account. Activity was measured by means of short-term pitfall trapping. The traps (∅ = 9.5 cm, formalin 10 % as fixative) were installed on a stony bank in line transects at different distances from the shore and emptied at dawn and just before sunrise during two consecutive days. Pitfall trapping only took place at the end of June beginning of July in 1987 and 1988 respectively with 36 and 54 sampling units.
In order to assess (1°) some body shape characteristics related to the degree of dorso-ventral flattening and (2°) the hind wing and flight muscle developmental state as measures of the dispersal power of the species populations concerned, biometry as well as dissection of the metathorax were performed on the collected beetles. We refer to DESENDER et al. (1986) for more details on these methods. Because members of different subgenera of the genus *Bembidion* (with more or less general size differences between subgenera) are involved in this study, the dorso-ventral flattening of the species is expressed as the proportion of the pronotal height to total body length. Other measurements or indices related to the dorso-ventral flattening of the hind body are subject to relatively larger measurements errors, because the hind body height is influenced by the reproductive state of each individual. As these indices revealed however no substantially different results as to their interpretation, their values are omitted here. Moreover, we preferred to use total body length because this character describes more general size differences between different species as compared to partial measures. Camera lucida drawings were made of the pronotum viewed from the rear in dorso-ventral plane in order to compare the profiles of the prothorax in the studied species with the results of the biometric analyses.
Wing morph frequencies were scored for large samples of two wing-dimorphic species included in this species-set and compared to values obtained for other habitats in our country (unpublished data).

Results and discussion

1) Microhabitat preference and environmental cues in habitat selection

The following species are treated in this paper: *Bembidion atrocoeruleum* STEPHENS, 1829, *B. decorum* ZENKER, 1801, *B. fluviatile* DEJEAN, 1831, *B. prasinum* (DUFTSCHMID, 1812), *B. properans* STEPHENS, 1829, *B. punctulatum* DRAPIEZ, 1820 and *B. tetracolum* SAY, 1823.
In general, *B. properans* and *B. tetracolum* are both known to be eurytopic carabid beetles with a preference for loamy to sandy loam soil. *B. properans* is most numerous in shortgrazed grasslands and only to a lesser degree riparian; *B. tetracolum* prefers more or less eutrophic riparian habitats, regularly with much detritus, as well as cultivated fields (cf. DESENDER, 1986). The remaining five species are much more stenotopic and confined to river banks with, according to the species, more or less coarse substrates and no or only very few vegetation (cf. DESENDER, 1986). Many of these species show a very restricted geographical distribution in our country as they are limited to banks or shores along non- or only slightly polluted rivers.
Fig. 1. compares the distribution of four of these species as deduced from pitfall trapping on banks along the river Ourthe. Other sampling campaigns yielded very comparable results.
B. tetracolum is especially abundant on the more sandy loam shore with detritus and vegetation, whereas *B. properans* has been caught in larger numbers on the edge of a stony river bank where the bank merges into a pasture. *B. fluviatile* is not figured here because it has only been caught in high numbers in yet another microhabitat, namely very steep to vertical slopes along the river where this species lives between loamy soil intermixed with narrow layers of stones. The four other species preferably occur on more or less stony river banks. Although the substrate of these banks can be quite homogeneously composed of mainly large stones, the distribution of the carabid species is not at all homogeneous. *B. decorum* clearly prefers the lowest zones, closest to the shore, whereas *B. atrocoeruleum* is more numerous higher up. The environmental cues related to the difference in microhabitat preference between these carabids are most probably directly or indirectly related to microclimate characteristics. Measurements of temperature and relative humidity (Fig. 2.) indeed show steep gradients across the shore, which are pronounced during very warm weather. *B. punctulatum* occurs also close to the shore line but in a microhabitat that differs from the one of the already



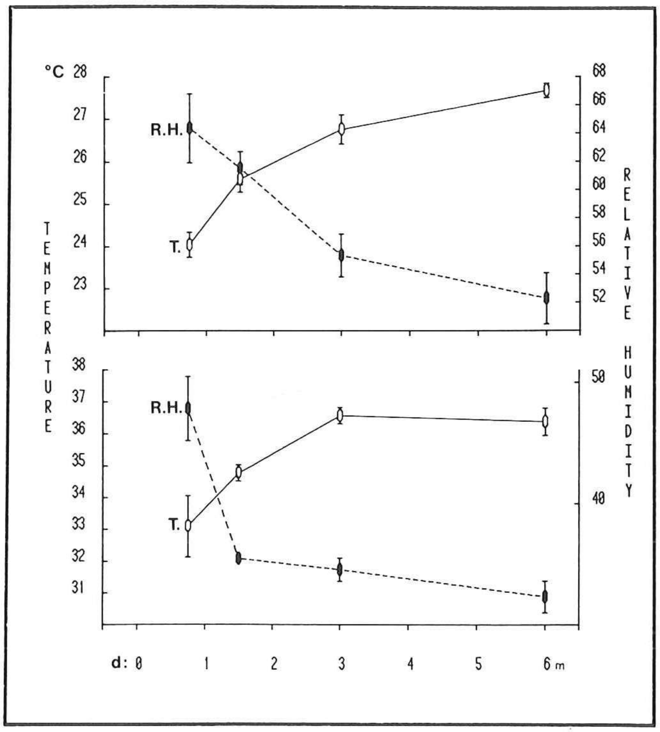
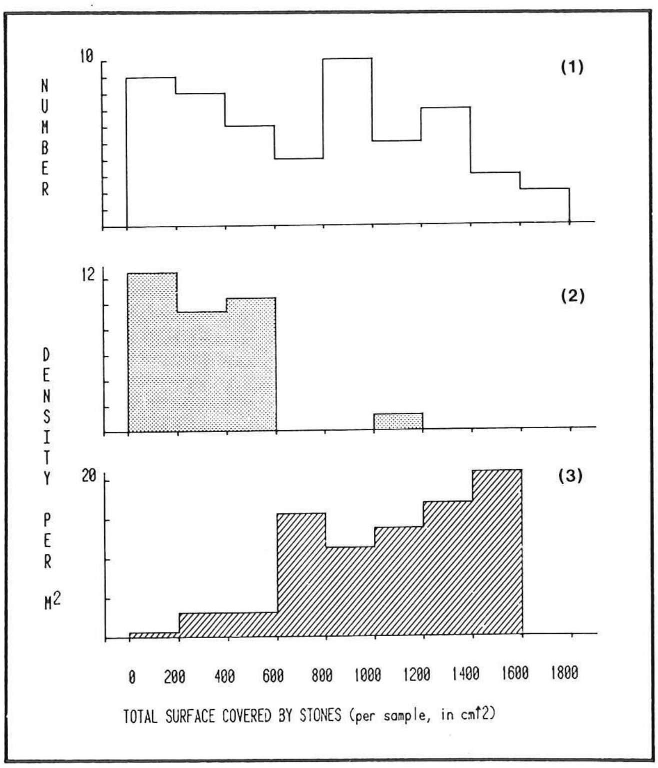


Fig. 1. Microhabitat distribution as deduced from short term pitfall trapping of 4 Bembidion*-species on banks of the river Ourthe; A = stony bank, B = loamy shore with detritus, vegetation and some stones; d = distance from the shore; 1 =* B. tetracolum, *2 =* B. properans, *3 =* B. atrocoeruleum, *4 =* B. decorum.

Fig 2 Temperature and relative humidity gradients on two days with different weather conditions at increasing distances from the shore of a stony bank (14hOO; soil surface).



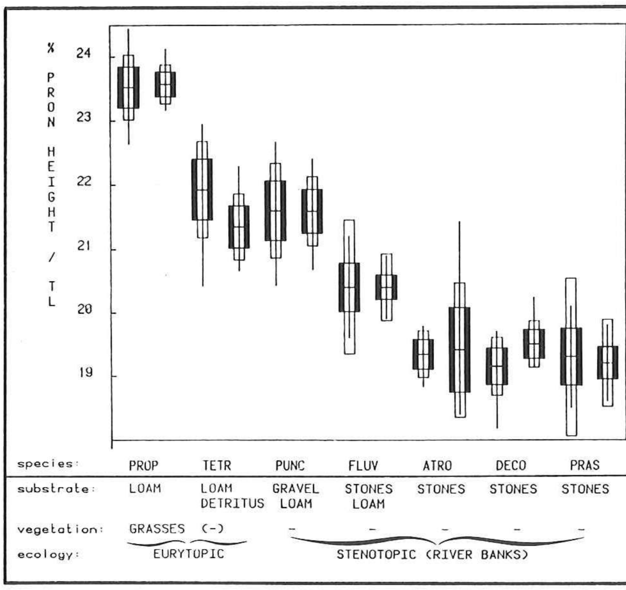


Fig. 3. Microhabitat frequency distribution of (2) Bembidion punctulatum *and (3)* B. decorum *densities as compared to the total surface covered by large stones in quadrat samples; the number of samples in each cell is shown in (1).*

Fig. 4. Range diagrams (mean values, 95 % c.l., 1 s.d. limits, range) of the degree of dorso-ventral flattening (% pronotal height / total body length) in the different species (males and females separately) arranged according to increasing size of substrate texture of their microhabitat (PROP = B. properans, *TETR =* B. tetracolum, *PUNC =* B. punctulatum, *FLUV =* B. fluviatile, *ATRO =* B. atrocoeruleum, *DECO =* B. decorum, *PRAS =* B. prasinum)

mentioned *B. decorum* : quadrat - flottation sampling combined with substrate analyses and measurements of all the stones at the soil surface in each sample show that *B. punctulatum* is especially abundant on shores with a relatively low total coverage by large stones in comparison with *B. decorum* (Fig. 3.). Shores with *B. punctulatum* mostly possess only a very faint slope and are partly covered by a thin loam layer. Finally, *B. prasinum* is only abundant very close to the shore. However, we deduced from timed handcatches that it occurs only on river banks with again a very faint slope but now mainly composed of large and superimposed stones.

2) Structure of the microhabitat and differences in body shape

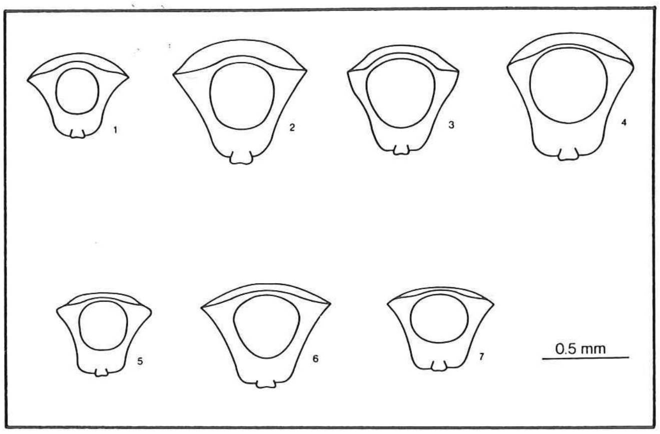
From the above-mentioned results we can rank the 7 *Bembidion*-species according to their preference for different substrates along an axis from fine to very coarse soil fractions (cf. Fig. 4). On this axis the three species to the right, namely *B. atrocoeruleum, B. decorum* and *B. prasinum,* all show an equally pronounced preference for a substrate with abundant large stones. The degree of dorso-ventral flattening of these beetles, expressed as the percentage of pronotal height to total body length, is plotted in Fig. 4. for males and females separately and in the same order as the species ranks just mentioned.
These species-range diagrams (with mean values, 95 % confidence limits, one standard deviation limits and total range added) obviously show a positive correlation between the degree of dorso-ventral flattening and a more pronounced lithophilous ecology of the species concerned. This corroborates the findings of ANDERSEN (1985) on other species of the genus. Both sexes yield very similar values. On species level, there are significant differences between the index values for *B. properans* and the remaining species, between *B. punctulatum, B. tetracolum* and the remaining species and finally between *B. fluviatile* and the remaining species. This indicates a fine tuning of body shape characteristics to subtile but significant differences in substrate features of the preferred microhabitat. Comparison of the pronotal profiles (Fig. 5.) shows a clear distinction between the pronounced lithophilous species and the other ones, especially in the degree to which the dorsal surface is flattened. Because all the lithophilous species belong to different subgenera, it appears that a flat body has strong adaptive value for the beetles in question. I.o.w., it seems to have developed undependently of phylogenetic relationships. This again corresponds to the results obtained by ANDERSEN (1985) but should be further tested through the analysis of other species.
The adaptive significance of a more flattened body for such species confined to stony shores and banks seems obvious : it allows the beetles to move more freely in this microhabitat, improving their efficiency to search for food, for the most suitable microclimatological conditions, a copulation partner or suitable reproductive sites and at the same time allows them to escape more easily from predators. It may also increase the possibilities for sheltering during inactive periods under or at the edges of stones. At the opposite end of this axis and in the absence of the suggested selection pressures we hypothesize that a more cylindric body shape is maintained by a smaller body surface/volume ratio.

3) Daytime activity and coloration of the elytra

In Table 1 we compare the percentages of activity during daytime with the coloration of the elytra in the same 7 *Bembidion* species. For some of the species the diel activity results are based on low numbers only, which means that these results have to be interpreted with caution. The results nevertheless suggest a clear relationship between the degree of metallic coloration and the amount of activity developed during daytime. Functionally, a metallic coloration could increase the amount of reflected light to reduce possible body overheating. This corroborates the results on other carabid species compiled by THIELE (1977), although spectra of reflected light have only been measured in very few carabids until now. In the near future we will try to take reflectospectrofotometric measurements in different species to assess the thermal properties of their integument on a quantitative basis.

4) Dispersal power and habitat characteristics

Table 1 also deals with the developmental state of the wings. As expected, the stenotopic riparian species all appear to be constantly macropterous. Dissections of the metathoracal indirect flight musculature show these species always to be in the possession of functional flight muscles; most species have indeed been observed flying, also during our sampling campaigns (see also LINDROTH, 1945; VAN HUIZEN, 1980). Escape flight activity could easily be induced by pouring water on the shores. These species therefore possess a high dispersal power, the adaptive value of which lies clearly in the possibility to escape from and recolonize their temporal habitat. Several riparian *Bembidion*-species have been reported also to show more or less seasonal migrations to and from winter quarters which are situated in higher zones along river valleys or riversides. MEISSNER (1983) for example observed this phenomenon in *B. punctulatum.* The occurrence of such seasonal migrations is probably linked to a more predictable instability due to higher water levels during Winter-early Spring; moreover these *Bembidion*-species all breed during Spring - early Summer, there new generation of beetles appearing in Summer-early Autumn. Whether functional flight muscles are also maintained or autolyzed during hibernation diapause has not yet been studied in



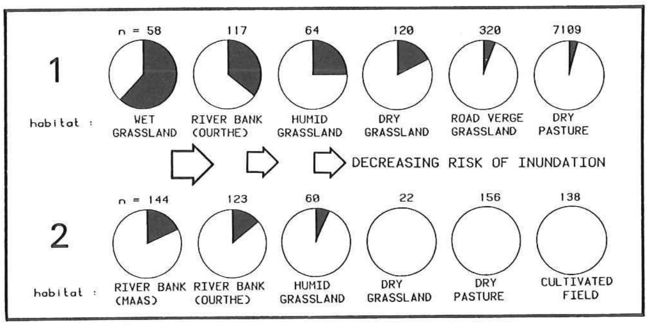


Fig. 5. Profiles of pronotum (dorso-ventral plane) in different Bembidion-*species (species rank cf. legend Fig. 4)*

Fig. 6. Wing morph frequencies in two wing dimorphic Bembidion-*species in different populations arranged according to decreasing risk of inundation of the habitat (1 =* B. properans, *2 =* B. tetracolum; *white sectors = brachypterous ind., black sectors = macropterous ind.)*

these riparian carabids. Some other ground beetles were already investigated in this respect and appear to autolyze and rebuild their flight muscles during and at the end of hibernation (e.g. VAN HUIZEN, 1977). The eurytopic species *B. properans* and *B. tetracolum* on the other hand are wing dimorphic carabids, with macropterous as well as brachypterous individuals occurring simultaneously in different populations. Wing morph frequencies of these species in different populations plotted along an axis indicating a decreasing risk of inundation of their habitat, show much higher proportions of macropterous individuals in populations occurring on sites where this risk is increased (Fig. 6.). In summary, the dispersal power of these *Bembidion*-species matches the unpredictable instability of their riparian habitats, i.o.w. individuals with a lower dispersal power are selected against in these situations.

5) Conclusions

We can conclude that micromorphological adaptations are indeed present along the investigated ecological axes. THIELE (1977) suggested that pronounced morphological adaptations of carabid beetles are associated only with burrowing, living under bark of trees or with feeding specializations. In his view the body structure in the large majority of carabids in no way indicates the reason for a particular habitat preference. However, he allowed for the possibility that species with similar body structure might be distinguishable at a micromorphological level. Our results show that this is indeed the case and that the ability to reveal such adaptations in carabids depends very much on the scale used by the investigator. To our opinion this is a wide and largely unexplored study field.

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species:	PROP	TETR	PUNC	FLUV	ATRO	DECO	PRAS
coloration of elytra:	BRONZE METALLIC	DULL	BRONZE ±METALLIC	DULL	BLUE ±METALLIC	DARK BLUE	DULL
daytime act.:	* 91%	11%	* 54%	10%	* 65%	* 42%	0%
n:	110	205	24	10	679	422	3
wings:	DIMORPHIC		CONSTANTLY MACROPTEROUS				
ecology:	EURYTOPIC		STENOTOPIC (RIVER BANKS)				

Table 1. Coloration of integument, percentage of daytime activity and wing developmental state in the different Bembidion-*species (abbreviations cf. legend Fig. 4)*

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